

A New Species of the Asian Leaf Litter Toad Genus *Leptobrachella* (Amphibia, Anura, Megophryidae) from Chongqing City, Southwest China

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Abstract Herein we describe a new species, *Leptobrachella yunyangensis* **sp. nov.**, from Yunyang County, Chongqing City, China, based on a combination of molecular and morphological data. Phylogenetic analysis based on the mitochondrial 16S rRNA gene and six nuclear genes indicated that this new species represented an independent evolutionary lineage. The uncorrected genetic distance between the new species and its closest congener species, *L. oshanensis*, was 5.4 % for 16S rRNA. The new species can be distinguished from its congeners by a combination of the following characters: (1) moderate body size (SVL 28.3–30.6 mm in males); (2) rough dorsal skin, with sparse large granules and tubercles and short longitudinal ridges on the shoulder; (3) distinctly discernible tympanum with a diameter smaller than that of the eye (TMP/EYE ratio: 0.51) and a distinct black supratympanic line present; (4) an internasal distance almost equal to interorbital distance (IND/IOD ratio: 1.05); (5) flanks with several dark spots arranged longitudinally in two rows; (6) distinctly visible supra-axillary, femoral, pectoral, and ventrolateral glands; (7) bicolored iris, with the upper 1/3 of the iris being copper orange and the lower 2/3 a light silvery grey;

(8) relative finger lengths of I < II = IV < III and relative toe lengths of I < II < V < III < IV; (9) absence of webbing and lateral fringes on fingers, and toes with rudimentary webbing and narrow lateral fringes; (10) heels overlapping when the thighs are positioned at right angles to the body; (11) tibiotarsal articulation reaching to the anterior corner of the eye when the leg is stretched forward; (12) ventral surfaces of the throat, chest, and belly greyish white with purple-brown speckling; (13) lacking distinct blackish dorsolateral markings; and (14) transverse dark brown bars on the surfaces of limbs and digits.

Keywords mitochondrial DNA, morphology, new species, nuclear gene, taxonomy

1. Introduction

The genus *Leptolalax* (Dubois, 1983) in the family Megophryidae (Bonaparte, 1850), is regarded as closely associated with the genus *Leptobrachella* (Smith, 1925) and has been assigned as a synonym of the genus *Leptobrachella* based on a large-scale molecular analysis (Chen *et al.*, 2018). Currently, the genus *Leptobrachella* contains 91 species (Frost, 2021; Chen *et al.*, 2021a) that are widely distributed from southern China to northeastern India and Myanmar, extending to mainland Indochina, peninsular Malaysia, and the island of Borneo (Fei *et al.*, 2012; Frost, 2021). *Leptobrachella* has a relatively high diversity of cryptic species, with nearly 59 species described since 2010 (see the *Leptobrachella* species list in Frost 2021; Chen *et al.*, 2021a). Currently, 33 species of this genus are known

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from China (AmphibiaChina, 2021). These are *L. alpina* (Fei, Ye and Li, 1990) and *L. bourreti* (Dubois, 1983) from Yunnan and Guangxi; *L. aspera* Wang, Lyu, Qi and Wang, 2020, *L. eos* (Ohler, Wollenberg, Grosjean, Hendrix, Vences, Ziegler and Dubois, 2011), *L. feii* Chen, Yuan and Che, 2020, *L. flaviglandulosa* Chen, Wang and Che, 2020, *L. nyx* (Ohler, Wollenberg, Grosjean, Hendrix, Vences, Ziegler and Dubois, 2011), *L. niveimontis* Chen, Poyarkov, Yuan and Che, 2020, *L. purpurus* (Yang, Zeng and Wang, 2018), *L. pelodytoides* (Boulenger, 1893), *L. tengchongensis* (Yang, Wang, Chen and Rao, 2016), and *L. yingjiangensis* (Yang, Zeng and Wang, 2018) from Yunnan; *L. laui* (Sung, Yang and Wang, 2014) and *L. yunkaiensis* (Wang, Li, Lyu and Wang, 2018) from southern Guangdong, including Hong Kong; *L. liui* (Fei and Ye, 1990) from Fujian, Jiangxi, Guangdong, Guangxi, Hunan, and Guizhou; *L. oshanensis* (Liu, 1950) from Gansu, Sichuan, Chongqing, Guizhou, and Hubei; *L. yuae* Shi, Hou, Song, Jiang and Wang, 2021 from Sichuan; *L. bashaensis* Lyu, Dai, Wei, He, Yuan, Shi, Zhou, Ran, Kuang, Guo, Wei and Yuan, 2020, *L. purpuraventra* Wang, Li, Li, Chen and Wang, 2019, *L. bijie* Wang, Li, Li, Chen and Wang, 2019, *L. sui yangensis* Luo, Xiao, Gao and Zhou, 2020, *L. chishuiensis* Li, Liu, Wei and Wang, 2020, *L. dorsospina* Wang, Lyu, Qi and Wang, 2020, and *L. jinshaensis* Cheng, Shi, Li, Liu, Li and Wang, 2021 from Guizhou; *L. ventripunctata* (Fei, Ye and Li, 1990) from Guizhou and Yunnan; *L. mangshanensis* (Hou, Zhang, Hu, Li, Shi, Chen, Mo and Wang, 2018), and *L. wulingensis* Qian, Xiao, Cao, Xiao and Yang, 2020 from southern Hunan and Guizhou, and *L. damingshanensis* Chen, Yu, Cheng, Meng, Wei, Zhou and Lu, 2021, *L. sungi* (Lathrop, Murphy, Orlov and Ho, 1998), *L. maoershanensis* (Yuan, Sun, Chen, Rowley and Che, 2017), *L. shangsiensis* Chen, Liao, Zhou and Mo, 2019, *L. shiwandashanensis* Chen, Peng, Pan, Liao, Liu and Huang, 2021, and *L. wuhuangmontis* Wang, Yang and Wang, 2018 from Guangxi (Fei *et al.*, 2012; Sung *et al.*, 2014; Yang *et al.*, 2016; Yuan *et al.*, 2017; Yang *et al.*, 2018; Wang *et al.*, 2018; Hou *et al.*, 2018; Chen *et al.*, 2019; Wang *et al.*, 2019, 2020; Chen *et al.*, 2018, 2020; Luo *et al.*, 2020; Lyu *et al.*, 2020; Li *et al.*, 2020; Qian *et al.*, 2020; Chen *et al.*, 2021a, b; Cheng *et al.*, 2021; Liu *et al.*, 2021; Shi *et al.*, 2021). The continual discovery of new species suggests that *Leptobranchella* species diversity may be grossly underestimated, and thus extensive field surveys by researchers are required.

During biodiversity surveys in Yunyang County, Chongqing, China, during June 2021, we collected several specimens of an unknown *Leptobranchella* species. The specimens were assigned to the genus *Leptobranchella* on the basis of the following characters: (1) a comparatively small body size, with a snout-vent length less than 60.0 mm; (2) having an elevated inner metacarpal tubercle; (3) having macro-glands on the body (including supra-axillary, femoral, and ventrolateral glands); (4) lacking vomerine teeth; (5) having small tubercles on the eyelids; (6) having a whitish vertical bar on the anterior tip of the snout (Dubois, 1983; Matsui, 1997, 2006; Lathrop *et al.*, 1998; Delorme *et al.*, 2006;

Das *et al.*, 2010). Subsequent phylogenetic analysis of mitochondrial genes and nuclear gene fragments revealed that these specimens belonged to the genus *Leptobranchella* and represented a distinct evolutionary lineage. Combining morphological data and molecular genetic differences, we describe the specimens as a new species.

2. Materials and Methods

2.1. Sampling A total of 12 new specimens were collected in this study. Six specimens were of the undescribed species from Qiyaoshan Nature Reserve and Lianhua Village, Renhe Town, Yunyang County, Chongqing, China; six were *L. alpina* from Wulian Mountain, Jingdong County, Yunnan, China. All specimens were fixed in 10% buffered formalin and later transferred to 75% ethanol for preservation. The muscle samples used for molecular analysis were preserved in 95% alcohol and stored at -20°C . All newly collected specimens were kept at Guizhou Normal University (GZNU), Guiyang City, Guizhou Province, China.

2.2. DNA extraction, PCR, and sequencing Genomic DNA was extracted from muscular tissue using a DNA extraction kit from Tiangen Biotech Co., Ltd. (Beijing, China). Seven tissue samples used for molecular analysis were amplified and sequenced for one mitochondrial gene and six nuclear genes: the partial 16S ribosomal RNA gene (16S rRNA), brain-derived neurotrophic factor (BDNF), sodium/calcium exchanger 1 (NCX), neurotrophin 3 (NTF3), recombination activating gene 1 (RAG1), rhodopsin (RHOD), and solute carrier family 8 member 3 (SLC8A3) (Primer sequences are in Table S1). PCR amplifications were performed in a 20 μl reaction volume with the following cycling conditions: an initial denaturing step at 95°C for 5 min, 35 cycles of denaturing at 95°C for 1 min, annealing at $50\text{--}57^{\circ}\text{C}$ for 1 min, and extending at 72°C for 1 min, followed by a final extending step at 72°C for 10 min. PCR products were purified with spin columns. The purified products were sequenced with both forward and reverse primers using a BigDye Terminator Cycle Sequencing Kit according to the guidelines of the manufacturer. The products were sequenced on an ABI Prism 3730 automated DNA sequencer at Chengdu TSING KE Biological Technology Co. Ltd (Chengdu, China). All newly obtained sequences have been submitted to GenBank (Table 1).

2.3. Phylogenetic analyses For the molecular analysis, we used 276 sequences from 79 species of the genus *Leptobranchella* for phylogenetic analysis, including 52 sequences newly amplified and sequenced from nine muscle tissue samples and 224 sequences downloaded from GenBank. In addition, we followed the methods of Chen *et al.* (2018) and selected *Leptobranchium huashen* (Fei and Ye, 2005), *Leptobranchium chapaense* (Bourret,

Table 1 Localities, voucher information, and GenBank numbers for all samples used in this study.

ID	Species	Locality	Voucher No.	GenBank No.						
				16S rRNA	BDNF	RAG1	RHOD	NCX	NTF3	SLC8A3
1	<i>Leptobrachella bijie</i>	Zhaozishan Nature Reserve, Bijie City, Guizhou, China	SYS a007314	MK414533	-	-	-	-	-	-
2	<i>Leptobrachella chishuiensis</i>	Chishui National Nature Reserve, Chishui City, Guizhou, China	CIBCS20190518042	MT117054	-	-	-	-	-	-
3	<i>Leptobrachella jinshaensis</i>	Lengshuihe Nature Reserve, Jinsha County, Guizhou, China	CIBJS20200516001	MT814014	-	-	-	-	-	-
4	<i>Leptobrachella suiyangensis</i>	Huoqiuba Nature Reserve, Suiyang County, Guizhou, China	GZNU20180606005	MK829649	OL800382	OL800396	OL800412	OL800373	OL800388	OL800399
5	<i>Leptobrachella suiyangensis</i>	Huoqiuba Nature Reserve, Suiyang County, Guizhou, China	GZNU20180606006	MK829650	OL800383	OL800397	OL800413	OL800374	OL800387	OL800398
6	<i>Leptobrachella suiyangensis</i>	Huoqiuba Nature Reserve, Suiyang County, Guizhou, China	GZNU20180606002	MK829648	OL800381	OL800395	OL800411	OL800372	OL800386	OL800400
7	<i>Leptobrachella purpuraventra</i>	Wujing Nature Reserve, Bijie City, Guizhou, China	SYS a007081	MK414517	-	-	-	-	-	-
8	<i>Leptobrachella niveimontis</i>	Daxueshan Nature Reserve, Yunnan, China	KIZ015734	MT302618	-	-	-	-	-	-
9	<i>Leptobrachella graminicola</i>	Mount Pu Ta Leng, Lao Cai, Vietnam	VNMN 010910	MZ224655	-	-	-	-	-	-
10	<i>Leptobrachella yeae</i>	Linggongli, Mount Emei, Sichuan, China	CIBEMGL19052104	MT957006	-	MT975979	-	-	-	-
11	<i>Leptobrachella bourreti</i>	Mao'er Shan, Guangxi, China	KIZ019389	MH055869	MH055981	MH056095	MH056138	MH056019	MH056057	MH056171
12	<i>Leptobrachella wulingensis</i>	Tianquanshan Forest Park, Zhangjiajie, Hunan, China	CSUFT 177	MT530315	OL800384	-	OL800414	OL800375	OL800389	OL800405
13	<i>Leptobrachella wulingensis</i>	Tianquanshan Forest Park, Zhangjiajie, Hunan, China	CSUFT 194	MT530316	OL800385	-	OL800415	OL800376	OL800390	OL800406
14	<i>Leptobrachella dorsospina</i>	Yushe Forest Park, Shuicheng County, Guizhou, China	SYS a004961	MW046194	-	-	-	-	-	-
15	<i>Leptobrachella alpina</i>	Caiyanghe, Yunnan, China	KIZ049024	MH055867	MH055979	MH056093	MH056142	MH056017	MH056055	MH056169
16	<i>Leptobrachella purpura</i>	Yingjiang, Yunnan Province, China	SYS a006530	MG520354	-	-	-	-	-	-
17	<i>Leptobrachella eos</i>	Boun Tay, Phongsaly, Laos	NCSM 80551	MH055887	-	-	-	-	-	-
18	<i>Leptobrachella oshanensis</i>	Emei Shan, Sichuan, China	Tissue ID: YPX37492	MH055896	MH055980	MH056094	MH056153	MH056018	MH056056	MH056170
19	<i>Leptobrachella yunyangensis</i> sp. nov.	Qiyaoshan Nature Reserve, Yunyang County, Chongqing, China	GZNU20210622001	OL800364	OL800377	OL800393	OL800407	OL800368	-	OL800401
20	<i>Leptobrachella yunyangensis</i> sp. nov.	Qiyaoshan Nature Reserve, Yunyang County, Chongqing, China	GZNU20210622002	OL800365	OL800378	OL800394	OL800408	OL800369	-	OL800402
21	<i>Leptobrachella yunyangensis</i> sp. nov.	Lianhua Village, Renhe Town, Yunyang County, Chongqing, China	GZNU20210622001	OL800366	OL800379	OL800391	OL800409	OL800370	-	OL800403
22	<i>Leptobrachella yunyangensis</i> sp. nov.	Lianhua Village, Renhe Town, Yunyang County, Chongqing, China	GZNU20210622003	OL800367	OL800380	OL800392	OL800410	OL800371	-	OL800404
23	<i>Leptobrachella tengchongensis</i>	Gaoligong Shan, Yunnan, China	SYS a004598	KU589209	-	-	-	-	-	-
24	<i>Leptobrachella khasiorum</i>	Khasi Hills, Meghalaya, India	SDBDU 2009.329	KY022303	-	KY022348	-	-	-	-
25	<i>Leptobrachella yingjiangensis</i>	Yingjiang, Yunnan, China	SYS a006533	MG520350	-	-	-	-	-	-

Continued Table 1

ID	Species	Locality	Voucher No.	GenBank No.						
				16S rRNA	BDNF	RAG1	RHOD	NCX	NTF3	SLC8A3
26	<i>Leptobranchella namdongensis</i>	Thanh Hoa Province, Vietnam	VNUF A.2017.37	MK965389	-	-	-	-	-	-
27	<i>Leptobranchella petrops</i>	Ba Vi National Park, Ha Tay, Vietnam	ROM 13483	MH055901	MH055978	MH056092	MH056150	MH056016	MH056054	MH056168
28	<i>Leptobranchella puhoatensis</i>	Pu Hu, Thanh Hoa, Vietnam	VNMN:2016 A.23	KY849587	-	-	-	-	-	-
29	<i>Leptobranchella liui</i>	Wuyi Shan, Fujian, China	SYS a001597	KM014547	-	-	-	-	-	-
30	<i>Leptobranchella mangshanensis</i>	Mangshan, Hunan, China	MSZTC201701	MG132196	-	-	-	-	-	-
31	<i>Leptobranchella yunkaiensis</i>	Dawuling Forest Station, Maoming City, Guangdong, China	SYS a004663	MH605584	-	-	-	-	-	-
32	<i>Leptobranchella bashaensis</i>	Basha Nature Reserve, Congjiang County, Guizhou, China	GIB196403	MW136294	-	-	-	-	-	-
33	<i>Leptobranchella maershanensis</i>	Mao'er Shan, Guangxi, China	KIZ07614	MH055927	MH055985	MH056099	MH056146	MH056023	MH056061	MH056175
34	<i>Leptobranchella laui</i>	Shenzhen, Guangdong, China	SYS a002450	MH055904	-	-	-	-	-	-
35	<i>Leptobranchella flaviglandulosa</i>	Xiaoqiaogou Nature Reserve, Yunnan, China	KIZ016072	MH055934	MH055984	MH056098	MH056135	MH056022	MH056060	MH056174
36	<i>Leptobranchella aspera</i>	Huanglianshan Nature Reserve, Lychun, Yunnan, China	SYS a007743	MW046199	-	-	-	-	-	-
37	<i>Leptobranchella feii</i>	Xiaoqiaogou Nature Reserve, Yunnan, China	KIZ048894	MT302634	-	-	-	-	-	-
38	<i>Leptobranchella pelodyroides</i>	Tam Dao, Vinh Phu, Vietnam	ROM18282	EF397244	-	-	-	-	-	-
39	<i>Leptobranchella ventripunctata</i>	Wenlong, Yunnan, China	KIZ013621	MH055824	MH055976	MH056090	MH056133	MH056014	MH056052	MH056166
40	<i>Leptobranchella aerea</i>	Vilabuly, Savannakhet, Laos	NCSM 76038	MH055809	-	-	-	-	-	-
41	<i>Leptobranchella minimus</i>	Doi Phu Fa, Nan, Thailand	KIZ024317	MH055852	MH055977	MH056091	MH056139	MH056015	MH056053	MH056167
42	<i>Leptobranchella nyx</i>	Ha Giang, Vietnam	ROM 36692	MH055816	-	-	-	-	-	-
43	<i>Leptobranchella shiwandashanensis</i>	Golden Camellia National Nature Reserve, Fangcheng City, Guangxi, China	NNU202103146	MZ326691	-	-	-	-	-	-
44	<i>Leptobranchella wuhuangmontis</i>	Mt. Wuhuang, Pubei County, Guangxi, China	SYS a003485	MH605577	-	-	-	-	-	-
45	<i>Leptobranchella pluvialis</i>	Fansipan, Lao Cai, Vietnam	ROM 30685	MH055843	-	-	-	-	-	-
46	<i>Leptobranchella nahangensis</i>	Na Hang Nature Reserve, Tuyen Quang, Vietnam	ROM 7035	MH055853	-	-	-	-	-	-
47	<i>Leptobranchella shangsiensis</i>	Guangxi, China	NHMG1401032	MK095460	-	-	-	-	-	-
48	<i>Leptobranchella firihii</i>	Quang Nam Province, Vietnam	AMS R 171714	JQ739203	-	-	-	-	-	-
49	<i>Leptobranchella isos</i>	Gia Lai, Vietnam	AMS R 176469	KT824767	-	-	-	-	-	-
50	<i>Leptobranchella sungi</i>	Tam Dao, Vinh Phuc, Vietnam	ROM 20236	MH055858	MH055990	MH056104	MH056151	MH056028	MH056066	MH056180
51	<i>Leptobranchella zhangyapingi</i>	Chiang Mai, Thailand	KIZ07258	MH055864	MH055988	MH056102	MH056144	MH056026	MH056064	MH056178
52	<i>Leptobranchella botsfordi</i>	Fansipan, Lao Cai, Vietnam	AMS R 176540	MH055952	MH055974	MH056088	MH056126	MH056012	MH056050	MH056164

Continued Table 1

ID	Species	Locality	Voucher No.	GenBank No.						
				16S rRNA	BDNF	RAG1	RHOD	NCX	NTF3	SLC8A3
53	<i>Leptobrachella kalonensis</i>	Binh Thuan Province, Vietnam	AMNH A191762	KR018115	-	-	-	-	-	-
54	<i>Leptobrachella pallida</i>	Vietnam: Lam Dong	UNS00511	KU530190	-	-	-	-	-	-
55	<i>Leptobrachella bidoupensis</i>	Bidoup-Nui Ba National Park, Lam Dong, Vietnam	ZMMU-A-4797-01454	MH055945	MH055996	MH056110	MH056155	MH056034	MH056072	MH056186
56	<i>Leptobrachella tudungensis</i>	Dak Nong Province, Vietnam	UNS00515	KR018121	-	-	-	-	-	-
57	<i>Leptobrachella maculosa</i>	Ninh Thuan Province, Vietnam	AMS R 177660	KR018119	-	-	-	-	-	-
58	<i>Leptobrachella pyrrhops</i>	Loc Bac, Lam Dong, Vietnam	ZMMU-A-4873-00158	MH055950	MH055995	MH056109	MH056156	MH056033	MH056071	MH056185
59	<i>Leptobrachella macrops</i>	Phu Yen, Vietnam	ZMMU-A5823	MG787993	-	-	-	-	-	-
60	<i>Leptobrachella applebyi</i>	Phong Dien Nature Reserve, Thua Thien-Hue, Vietnam	KIZO10701	MH055947	MH055991	MH056105	MH056130	MH056029	MH056067	MH056181
61	<i>Leptobrachella melica</i>	Cambodia, Ratanakiri	MVZ258198	HM133600	-	-	-	-	-	-
62	<i>Leptobrachella ardens</i>	Kon Ka Kinh National Park, Gia Lai, Vietnam	ZMMU-NAP-06099	MH055949	MH055994	MH056108	MH056162	MH056032	MH056070	MH056184
63	<i>Leptobrachella tuberosa</i>	Kon Ka Kinh National Park, Gia Lai, Vietnam	ZMMU-NAP-02275	MH055959	MH055997	MH056111	MH056160	MH056035	MH056073	MH056187
64	<i>Leptobrachella crocea</i>	Thua Thien-Hue, Vietnam	ZMMU-NAP-02274	MH055955	MH056000	MH056114	MH056159	MH056038	MH056076	MH056190
65	<i>Leptobrachella dringi</i>	Gunung Mulu, Malaysia	KUHE:55610	AB847553	-	-	-	-	-	-
66	<i>Leptobrachella sabahmontana</i>	Borneo, Malaysia	BORNEENSIS 12632	AB847551	-	-	-	-	-	-
67	<i>Leptobrachella fritiniensis</i>	Danum Valley Field Center, Sabah, Malaysia	FMNH 244800	MH055971	MH056004	MH056118	MH056127	MH056042	MH056080	MH056194
68	<i>Leptobrachella picta</i>	Borneo, Malaysia	UNIMAS 8705	KJ831295	-	-	-	-	-	-
69	<i>Leptobrachella hamidi</i>	Bukit Lanjan, Selangor, Malaysia	KUHE17545	AB969286	-	-	-	-	-	-
70	<i>Leptobrachella marmorata</i>	Borneo, Malaysia	KUHE53227	AB969289	-	-	-	-	-	-
71	<i>Leptobrachella gracilis</i>	Bukit Kana, Sarawak, Malaysia	FMNH 273682	MH055972	MH056003	MH056117	MH056128	MH056041	MH056079	MH056193
72	<i>Leptobrachella maura</i>	Borneo, Malaysia	SP21450	AB847559	-	-	-	-	-	-
73	<i>Leptobrachella fuliginosa</i>	Phetchaburi, Thailand	KUHE 20197	LC201988	-	-	-	-	-	-
74	<i>Leptobrachella melanoleucus</i>	Kapoe, Ranong, Thailand	KIZO18031	MH055967	MH056001	MH056115	MH056136	MH056039	MH056077	MH056191
75	<i>Leptobrachella neangi</i>	Veal Veng District, Pursat Province, Cambodia	CBC 1624	MT644613	-	-	-	-	-	-
76	<i>Leptobrachella brevicrus</i>	Gunung Mulu National Park, Sarawak, Malaysia	UNIMAS 8957	KJ831303	-	-	-	-	-	-
77	<i>Leptobrachella titokai</i>	Mulu National Park, Sarawak, Malaysia	KUHE:55897	LC137805	MH056006	MH056120	MH056149	MH056044	MH056082	MH056196
78	<i>Leptobrachella parva</i>	Mulu National Park, Sarawak, Malaysia	KUHE:55308	LC056791	MH056007	MH056121	MH056148	MH056045	MH056083	MH056197
79	<i>Leptobrachella baluensis</i>	Tambunan, Sabah, Borneo, Malaysia	SP 21604	LC056792	-	-	-	-	-	-

Continued Table 1

ID	Species	Locality	Voucher No.	GenBank No.						
				16S rRNA	BDNF	RAG1	RHOD	NCX	NTF3	SLC8A3
80	<i>Leptobrachella mjobergi</i>	Gading NP, Sarawak, Borneo, Malaysia	KUHE-47872	LC056787	-	-	-	-	-	-
81	<i>Leptobrachella julianiringi</i>	Mulu NP, Sarawak, Borneo, Malaysia	KUHE 55333	LC056780	-	-	-	-	-	-
82	<i>Leptobrachella heteropus</i>	Larut, Perak, Malaysia	KUHE15487	AB530453	-	-	-	-	-	-
83	<i>Leptobrachella solus</i>	Gunung Stong, Kelantan, Malaysia	KU RMB20973	MH055973	MH056005	MH056119	MH056147	MH056043	MH056081	MH056195
84	<i>Leptobrachella kecil</i>	Cameron, Malaysia	KUHE 52440	LC202004	-	-	-	-	-	-
85	<i>Leptobrachella kajangensis</i>	Tioman, Malaysia	LSUHC 4431	LC202001	-	-	-	-	-	-
86	<i>Leptobrachium boringii</i>	Sichuan, China	Tissue ID: YPX37539	KX811930	MH056009	MH056123	MH056154	MH056047	MH056085	MH056199
87	<i>Leptobrachium huashen</i>	Yunnan, China	KIZ049025	KX811931	MH056008	MH056122	MH056143	MH056046	MH056084	MH056198
88	<i>Megophrys glandulosa</i>	Yunnan, China	KIZ048439	KX811762	MH056011	MH056125	MH056141	MH056049	MH056087	MH056201

1937), and *Megophrys major* (Boulenger, 1908) as outgroups and downloaded 21 sequences from GenBank (Table 1).

For the phylogenetic analysis, we constructed two sequence matrices for reconstructing the phylogenetic tree, i.e., mitochondrial 16S rRNA and the combined sequences of six nuclear genes. All of the sequences were assembled and aligned using the MUSCLE (Edgar, 2004) module in MEGA 7.0 (Kumar *et al.*, 2016) with default settings. Alignments were checked by eye and revised manually if necessary. Trimming with the gaps partially deleted was performed in GBLOCKS 0.91b (Castresana, 2000). Phylogenetic analysis of the two sequence matrices was performed using maximum likelihood (ML) and Bayesian inference (BI). The best-fit nucleotide substitution models for the sequence supermatrices were selected in PartitionFinder 2.1.1 (Lanfear *et al.*, 2016) using the Bayesian information criterion (BIC). The results indicated GTR + I + G as the best-fitting nucleotide substitution model for the 16S rRNA sequence matrix, and K80+I+G (from SLC8A3 and RAG1), HKY+I+G (from NTF3, RHOD, and NCX), and K80+I (from BDNF) as the best-fitting nucleotide substitution models for the combined nuclear gene sequence matrix. Phylogenetic analysis using maximum likelihood (ML) and Bayesian inference (BI) methods was implemented in IQ-tree 2.0.4 (Nguyen *et al.*, 2015) and MrBayes 3.2.1 (Ronquist *et al.*, 2012), respectively. The ML analysis was run using the best-fit model for each partition with 2000 ultrafast bootstrap (UFB) replicates (Minh *et al.*, 2013), and was performed until a correlation coefficient of at least 0.99 was reached (Hoang *et al.*, 2018). For BI analyses, two independent runs were performed with four Markov chains (three heated chains and a single cold chain) based on the best-fit partitioning schemes and corresponding substitution models selected. Starting from a random tree, each run consisted of a total of 1×10^7 generations, sampled every 1000 generations. Convergence was assessed by the average standard deviation of split frequencies (ASDSF) being less than 0.01, and the effective sample sizes (ESS) being greater than 200 in Tracer 1.7.1 (Rambaut *et al.*, 2014). Nodes in the trees were considered well supported when Bayesian posterior probabilities (BPP) were ≥ 0.95 and ML ultrafast bootstrap (UFB) values were $\geq 95\%$. Finally, genetic distance between species via the uncorrected *P*-distance model for the 16S rRNA gene was estimated using MEGA 7.0.

2.4. Morphological and morphometric analyses Morphometric data were taken from six of the most well-preserved adult specimens (Table 2). Measurements were recorded to the nearest 0.1 mm using digital calipers following the methods of Fei *et al.* (2009) and Rowley *et al.* (2013). These measurements were as follows: **SVL** = snout-vent length (from tip of snout to vent); **HDL** = head length (from tip of snout to rear of jaws); **HDW** = head width (head width at the commissure of the jaws); **SNT** = snout length (from tip of snout to the anterior corner of the eye); **EYE** = eye diameter (diameter of the exposed portion of

Table 2 Measurements of the adult specimens of *Leptobrachella yunyangensis* **sp. nov.** All units in mm. See abbreviations for the morphological characters in the Materials and Methods section. *for the holotype.

Voucher	GZNU 20210629001*	GZNU 20210622001	GZNU 20210622002	GZNU 20210622003	GZNU 20210622004	GZNU 20210622005
Sex	Male	Male	Male	Male	Male	Male
SVL	30.6	28.3	27.9	29.2	29.8	29.9
HDL	11.1	9.1	10.2	10.8	11.2	11.6
HDW	9.8	9.6	9.6	10.1	10.6	10.6
SNT	4.9	4.3	4.3	4.8	4.6	4.2
EYE	3.5	3.3	3.7	3.1	3.6	3.5
IOD	4.1	3.5	3.3	3.8	3.5	3.4
IND	3.5	3.3	3.5	3.6	3.3	3.4
UEW	2.4	2.7	2.8	2.3	2.6	2.5
NEL	2.2	2.9	2.9	2.5	2.9	2.8
TMP	1.8	1.5	1.9	1.4	1.9	1.9
TEY	1.4	1.3	1.3	1.9	1.8	1.6
HND	7.5	7.5	7.3	7.1	7.7	7.5
LAHL	14.4	13.8	13.8	13.6	13.7	13.8
LW	2.5	1.5	1.2	1.4	1.3	1.4
HLL	48.9	49.8	42.6	45.4	49.6	46.6
THL	13.8	12.3	12.5	12.6	12.3	12.3
TIB	15.2	13.8	14.5	14.3	15.3	14.8
TW	4.3	4.1	4.4	4.8	4.4	4.6
FOT	13.8	13.2	13.5	13.6	13.7	13.9
TFL	19.9	18.6	20.6	20.8	19.9	19.2
IPTL	1.5	1.4	1.6	1.5	1.5	1.7
OPTL	0.9	0.7	0.8	0.9	0.8	0.7
IMTL	0.9	1.4	1.2	1.5	1.7	1.9

the eyeballs); **IOD** = interorbital distance (minimum distance between upper eyelids); **IND** = internasal distance (distance between nares); **UEW** = upper eyelid width (measured as the greatest width of the upper eyelid); **NEL** = nostril-eyelid length (distance from nostril to eyelid); **TMP** = tympanum diameter (horizontal diameter of the tympanum); **TEY** = tympanum-eye distance (distance from anterior edge of the tympanum to posterior corner of the eye); **HND** = hand length (distance from distal end of radioulna to tip of phalanx of finger III); **LAHL** = length of the lower arm and hand (distance from tip of the third finger to elbow); **LW** = lower arm width (maximum width of the lower arm); **HLL** = hindlimb length (distance from tip of fourth toe to vent); **THL** = thigh length (distance from vent to knee); **TIB** = tibia length (distance from knee to heel); **TW** = maximal tibia width; **FOT** = foot length (from proximal edge of the inner metatarsal tubercle to the tip of the fourth toe); **TFL** = length of foot and tarsus (distance from the tibiotarsal articulation to the distal end of toe IV); **IPTL** = inner palmar tubercle length (measured as maximal distance from

proximal to distal ends of the inner palmar tubercle); **OPTL** = outer metacarpal tubercle length (measured as maximal diameter of the outer metacarpal tubercle); and **IMTL** = inner metatarsal tubercle length (taken as maximal length of the inner metatarsal tubercle).

To reduce the impact of allometry, the correct value from the ratio of each character to SVL was calculated, and then all data were log-transformed (\log_{10}) for the subsequent morphometric analyses. Principal component analyses (PCAs) of size-corrected measurements and simple bivariate scatterplots were used to explore and characterize the morphometric differences between the undescribed species and *L. oshanensis*. Mann–Whitney *U* tests were conducted to determine the significance of differences in morphometric characters between the undescribed species and *L. oshanensis* in males. All statistical analyses were performed using SPSS 21.0 (SPSS, Inc., Chicago, IL, USA), and differences were considered statistically significant at $P < 0.05$.

Sex was determined by the presence of internal vocal sac openings, and the presence of eggs in the abdomen through

external inspection. Comparative morphological data for species of the genus *Leptobrachella* were obtained from the literature (Table 3). Owing to the high likelihood of undiagnosed diversity within the genus (Rowley *et al.*, 2016; Yang *et al.*, 2016), where available we relied on examination of topotypic material and/or original species descriptions. We also examined the type and/or topotype materials for *L. alpina*, *L. suiyangensis*, and *L. wulingensis* (Appendix).

3. Results

3.1. Phylogenetic analyses and genetic divergence

Phylogenetic trees from maximum likelihood (ML) and Bayesian inference (BI) were reconstructed based on DNA sequences of the mitochondrial 16S rRNA gene with a length of 532 base pairs (bp). In the 16S rRNA gene trees, two *Leptobrachella* populations from Yunyang County, Chongqing, China, clustered into a separate evolutionary lineage and were highly supported (1.00 in BI and 99 % in ML; Figure 1).

The analysis of the combined six nuclear loci (3594 bp in total length) (BDNF: 426 bp; RHOD: 321 bp; NCX: 426 bp; SLC8A3: 540 bp; RAG1: 1035 bp; NTF3: 567 bp) well resolved the phylogenetic relationships between the major clades of the genus *Leptobrachella* (Figure 2). These topologies differed from the matrilineal tree due to the lack of sufficient species. However, the two populations of the new species clustered into a highly independent evolutionary lineage that formed a sister clade with *L. oshanensis* (1.00 in BI and 100 % in ML; Figure 2).

The smallest pairwise genetic divergence between the population from Yunyang County, Chongqing, China, and 78 species of the genus *Leptobrachella* was 4.8% (*vs. L. bourreti*) to 20.4% (*vs. L. kecil*). These levels were similar or higher to the divergence among recognized congeners; for example, 1.9% between *L. bijie* and *L. chishuiensis* and 2.9 % between *L. aspera* and *L. feii* (Table S2). In conclusion, the genetic divergence, matrilineal tree, and nuclear gene tree were all highly supportive of the two *Leptobrachella* populations in Yunyang County, Chongqing, China, as an independent evolutionary lineage.

3.2. Morphological analyses The results of the Mann–Whitney *U* tests indicated that males of the new species differed significantly from *L. oshanensis* based on several morphometric characters, including SNT, IOD, IND, NEL, LW, TIB, TW, and FOT (all *P*-values < 0.05; Table 4). For the male group, PCA extracted three principal component axes with eigenvalues greater than two, and the percentages of explained variance of the first three principal components were 31.18%, 15.91%, and 12.25%, respectively, with a cumulative percentage of 60.33% (Table S3). There were 13 major morphological characteristics in the first three principal components that were mainly

distributed in the head and hind limbs (Table S3). The first two principal components explained 48.08% of the total variation in male morphology. In the PCA plot composed of PC 1 and PC 2, the first principal component axis could separate the new species from *L. oshanensis* (Figure 3) and was based on SNT, IOD, IND, TEY, TIB, and TW. The second component axis was based on UEW, HND, and LAHL. Based on the genetic and morphological differences, we describe the specimens here as a new species.

3.3. Taxonomy accounts

***Leptobrachella yunyangensis* sp. nov.** Luo, Deng and Zhou

Table 2; Figures 4–6

Holotype GZNU20210629001, adult male collected by Tao Luo on 29 June 2021 from the Lianhua Village, Renhe Town, Yunyang County, Chongqing, China (108.614642°N, 31.01610562°E, 908 mas.l.).

Paratypes GZNU20210622001, adult male collected from Qiyaoshan Nature Reserve, Yunyang County, Chongqing, China, by Tao Luo on June 22, 2021; GZNU20210622002–005, four adult males collected from Qiyaoshan Nature Reserve, Yunyang County, Chongqing, China (108.78942255°N, 30.6896741°E, 839 mas.l.), by Tao Luo and Dong Peng.

Etymology The specific epithet *yunyangensis* is in reference to the type locality, Lianhua Village, Renhe Town, Yunyang County, Chongqing, China. For the common name, we suggest “Guishi Leaf Litter Toad”, and for the Chinese name “Gui Shi Zhang Tu Chan (贵师掌突蟾)”. The year 2021 marks the 80th anniversary of the founding of Guizhou Normal University, which has made outstanding contributions to the training of teachers in Guizhou Province and the promotion of zoological research in China, and I would like to express my heartfelt wishes to Guishi, which comes from the abbreviation of Guizhou Normal University.

Diagnosis *Leptobrachella yunyangensis* sp. nov. can be distinguished from its congeners by a combination of the following characters: (1) moderate body size (SVL 28.3–30.6 mm in males); (2) rough dorsal skin, with sparse large granules and tubercles and short longitudinal ridges on the shoulder; (3) distinctly discernible tympanum with a diameter smaller than that of the eye (TMP/EYE ratio: 0.51) and a distinct black supratympanic line present; (4) an internasal distance almost equal to interorbital distance (IND/IOD ratio: 1.05); (5) flanks with several dark spots arranged longitudinally in two rows; (6) distinctly visible supra-axillary, femoral, pectoral, and ventrolateral glands; (7) bicolored iris, with the upper 1/3 of the iris being copper orange and the lower 2/3 a light silvery grey; (8) relative finger lengths of I < II = IV < III and relative toe lengths of I < II < V < III < IV; (9) absence of webbing and lateral fringes on fingers, and toes with rudimentary webbing and narrow lateral fringes; (10) heels overlapping when the

Table 3 References for morphological characters for congeners of the genus *Leptobrachella*.

ID	<i>Leptobrachella</i> species	Literature obtained
1	<i>L. aerea</i> (Rowley, Stuart, Richards, Phimmachak and Sivongxay, 2010)	Rowley <i>et al.</i> , 2010c
2	<i>L. alpina</i> (Fei, Ye and Li, 1990)	Fei <i>et al.</i> , 2009
3	<i>L. applebyi</i> (Rowley and Cao, 2009)	Rowley and Cao, 2009
4	<i>L. arayai</i> (Matsui, 1997)	Matsui, 1997
5	<i>L. ardens</i> (Rowley, Tran, Le, Dau, Peloso, Nguyen, Hoang, Nguyen and Ziegler, 2016)	Rowley <i>et al.</i> , 2016
6	<i>L. aspera</i> Wang, Lyu, Qi and Wang, 2020	Wang <i>et al.</i> , 2020
7	<i>L. baluensis</i> Smith, 1931	Dring, 1983; Eto <i>et al.</i> , 2016
8	<i>L. bashaensis</i> Lyu, Dai, Wei, He, Yuan, Shi, Zhou, Ran, Kuang, Guo, Wei and Yuan, 2020	Lyu <i>et al.</i> , 2020
9	<i>L. bidoupensis</i> (Rowley, Le, Tran and Hoang, 2011)	Rowley <i>et al.</i> , 2011
10	<i>L. bijie</i> Wang, Li, Li, Chen and Wang, 2019	Wang <i>et al.</i> , 2019
11	<i>L. bondangensis</i> Eto, Matsui, Hamidy, Munir and Iskandar, 2018	Eto <i>et al.</i> , 2018
12	<i>L. botsfordi</i> (Rowley, Dau and Nguyen, 2013)	Rowley <i>et al.</i> , 2013
13	<i>L. bourreti</i> (Dubois, 1983)	Ohler <i>et al.</i> , 2011
14	<i>L. brevicrus</i> Dring, 1983	Dring, 1983; Eto <i>et al.</i> , 2015
15	<i>L. chishuiensis</i> Li, Liu, Wei, and Wang, 2020	Li <i>et al.</i> , 2020
16	<i>L. crocea</i> (Rowley, Hoang, Le, Dau and Cao, 2010)	Rowley <i>et al.</i> , 2010a
17	<i>L. damingshanensis</i> Chen, Yu, Cheng, Meng, Wei, Zhou and Lu, 2021	Chen <i>et al.</i> , 2021a
18	<i>L. dorsospina</i> Wang, Lyu, Qi and Wang, 2020	Wang <i>et al.</i> , 2020
19	<i>L. dringi</i> (Dubois, 1987)	Inger <i>et al.</i> , 1995; Matsui and Dehling, 2012
20	<i>L. eos</i> (Ohler, Wollenberg, Grosjean, Hendrix, Vences, Ziegler and Dubois, 2011)	Ohler <i>et al.</i> , 2011
21	<i>L. feii</i> Chen, Yuan and Che, 2020	Chen <i>et al.</i> , 2020
22	<i>L. firthi</i> (Rowley, Hoang, Dau, Le and Cao, 2012)	Rowley <i>et al.</i> , 2012
23	<i>L. flaviglandulosa</i> Chen, Wang and Che, 2020	Chen <i>et al.</i> , 2020
24	<i>L. fritinniens</i> (Dehling and Matsui, 2013)	Dehling and Matsui, 2013
25	<i>L. fuliginosa</i> (Matsui, 2006)	Matsui, 2006
26	<i>L. fusca</i> Eto, Matsui, Hamidy, Munir and Iskandar, 2018	Eto <i>et al.</i> , 2018
27	<i>L. gracilis</i> (Günther, 1872)	Günther, 1872; Dehling, 2012b
28	<i>L. graminicola</i> Nguyen, Tapley, Nguyen, Luong and Rowley, 2021	Nguyen <i>et al.</i> , 2021
29	<i>L. hamidi</i> (Matsui, 1997)	Matsui, 1997
30	<i>L. heteropus</i> (Boulenger, 1900)	Boulenger, 1900
31	<i>L. isos</i> (Rowley, Stuart, Neang, Hoang, Dau, Nguyen and Emmett, 2015)	Rowley <i>et al.</i> , 2015a
32	<i>L. itiokai</i> Eto, Matsui and Nishikawa, 2016	Eto <i>et al.</i> , 2016
33	<i>L. jinshaensis</i> Cheng, Shi, Li, Liu, Li and Wang, 2021	Cheng <i>et al.</i> , 2021
34	<i>L. juliandringi</i> Eto, Matsui and Nishikawa, 2015	Eto <i>et al.</i> , 2015
35	<i>L. kajangensis</i> (Grismer, Grismer and Youmans, 2004)	Grismer <i>et al.</i> , 2004
36	<i>L. kalonensis</i> (Rowley, Tran, Le, Dau, Peloso, Nguyen, Hoang, Nguyen and Ziegler, 2016)	Rowley <i>et al.</i> , 2016
37	<i>L. kecil</i> (Matsui, Belabut, Ahmad and Yong, 2009)	Matsui <i>et al.</i> , 2009
38	<i>L. khasiorum</i> (Das, Tron, Rangad and Hooroo, 2010)	Das <i>et al.</i> , 2010
39	<i>L. lateralis</i> (Anderson, 1871)	Anderson, 1871; Humtsoe <i>et al.</i> , 2008
40	<i>L. laui</i> (Sung, Yang and Wang, 2014)	Sung <i>et al.</i> , 2014
41	<i>L. liui</i> (Fei and Ye, 1990)	Fei <i>et al.</i> , 2009; Sung <i>et al.</i> , 2014
42	<i>L. macrops</i> (Duong, Do, Ngo, Nguyen and Poyarkov, 2018)	Duong <i>et al.</i> , 2018
43	<i>L. maculosa</i> (Rowley, Tran, Le, Dau, Peloso, Nguyen, Hoang, Nguyen and Ziegler, 2016)	Rowley <i>et al.</i> , 2016
44	<i>L. mangshanensis</i> (Hou, Zhang, Hu, Li, Shi, Chen, Mo and Wang, 2018)	Hou <i>et al.</i> , 2018
45	<i>L. maoershanensis</i> (Yuan, Sun, Chen, Rowley and Che, 2017)	Yuan <i>et al.</i> , 2017

Continued Table 3

ID	<i>Leptobranchella</i> species	Literature obtained
46	<i>L. marmorata</i> (Matsui, Zainudin and Nishikawa, 2014)	Matsui <i>et al.</i> , 2014b
47	<i>L. maura</i> (Inger, Lakim, Biun and Yambun, 1997)	Inger <i>et al.</i> , 1997
48	<i>L. melanoleuca</i> (Matsui, 2006)	Matsui, 2006
49	<i>L. melica</i> (Rowley, Stuart, Neang and Emmett, 2010)	Rowley <i>et al.</i> , 2010b
50	<i>L. minima</i> (Taylor, 1962)	Taylor, 1962; Ohler <i>et al.</i> , 2011
51	<i>L. mjobergi</i> Smith, 1925	Eto <i>et al.</i> , 2015
52	<i>L. murphyi</i> Chen, Suwannapoom, Wu, Poyarkov, Xu, Pawangkhanant and Che, 2021	Chen <i>et al.</i> , 2021c
53	<i>L. nahangensis</i> (Lathrop, Murphy, Orlov and Ho, 1998)	Lathrop <i>et al.</i> , 1998
54	<i>L. namdongensis</i> Hoang, Nguyen, Luu, Nguyen and Jiang, 2019	Van <i>et al.</i> , 2019
55	<i>L. natunae</i> (Günther, 1895)	Günther, 1895
56	<i>L. neangi</i> Stuart and Rowley, 2020	Stuart and Rowley, 2020
57	<i>L. niveimontis</i> Chen, Poyarkov, Yuan and Che, 2020	Chen <i>et al.</i> , 2020
58	<i>L. nokrekensis</i> (Mathew and Sen, 2010)	Mathew and Sen, 2010
59	<i>L. nyx</i> (Ohler, Wollenberg, Grosjean, Hendrix, Vences, Ziegler and Dubois, 2011)	Ohler <i>et al.</i> , 2011
60	<i>L. oshanensis</i> (Liu, 1950)	Fei <i>et al.</i> , 2009
61	<i>L. pallida</i> (Rowley, Tran, Le, Dau, Peloso, Nguyen, Hoang, Nguyen and Ziegler, 2016)	Rowley <i>et al.</i> , 2016
62	<i>L. palmata</i> Inger and Stuebing, 1992	Inger and Stuebing, 1992
63	<i>L. parva</i> Dring, 1983	Dring, 1983
64	<i>L. pelodytoides</i> (Boulenger, 1893)	Boulenger, 1893; Ohler <i>et al.</i> , 2011
65	<i>L. petrops</i> (Rowley, Dau, Hoang, Le, Cutajar and Nguyen, 2017)	Rowley <i>et al.</i> , 2017a
66	<i>L. picta</i> (Malkmus, 1992)	Malkmus, 1992
67	<i>L. platycephala</i> (Dehling, 2012)	Dehling, 2012a
68	<i>L. pluvialis</i> (Ohler, Marquis, Swan and Grosjean, 2000)	Ohler <i>et al.</i> , 2000, 2011
69	<i>L. puhoatensis</i> (Rowley, Dau and Cao, 2017)	Rowley <i>et al.</i> , 2017b
70	<i>L. purpuraventra</i> Wang, Li, Li, Chen and Wang, 2019	Wang <i>et al.</i> , 2019
71	<i>L. purpureus</i> (Yang, Zeng and Wang, 2018)	Yang <i>et al.</i> , 2018
72	<i>L. pyrrhops</i> (Poyarkov, Rowley, Gogoleva, Vassilieva, Galoyan and Orlov, 2015)	Poyarkov <i>et al.</i> , 2015
73	<i>L. rowleyae</i> (Nguyen, Poyarkov, Le, Vo, Ninh, Duong, Murphy and Sang, 2018)	Nguyen <i>et al.</i> , 2018
74	<i>L. sabahmontana</i> (Matsui, Nishikawa and Yambun, 2014)	Matsui <i>et al.</i> , 2014a
75	<i>L. serasanae</i> Dring, 1983	Dring, 1983
76	<i>L. shangsiensis</i> Chen, Liao, Zhou and Mo, 2019	Chen <i>et al.</i> , 2019
77	<i>L. shiwandashanensis</i> Chen, Peng, Pan, Liao, Liu and Huang, 2021	Chen <i>et al.</i> , 2021b
78	<i>L. sola</i> (Matsui, 2006)	Matsui, 2006
79	<i>L. sungi</i> (Lathrop, Murphy, Orlov and Ho, 1998)	Lathrop <i>et al.</i> , 1998
80	<i>L. sui yangensis</i> Luo, Xiao, Gao and Zhou, 2020	Luo <i>et al.</i> , 2020
81	<i>L. tadungensis</i> (Rowley, Tran, Le, Dau, Peloso, Nguyen, Hoang, Nguyen and Ziegler, 2016)	Rowley <i>et al.</i> , 2016
82	<i>L. tamdil</i> (Sengupta, Sailo, Lalremsanga, Das and Das, 2010)	Sengupta <i>et al.</i> , 2010
83	<i>L. tengchongensis</i> (Yang, Wang, Chen and Rao, 2016)	Yang <i>et al.</i> , 2016
84	<i>L. tuberosa</i> (Inger, Orlov and Darevsky, 1999)	Inger <i>et al.</i> , 1999
85	<i>L. ventripunctata</i> (Fei, Ye and Li, 1990)	Fei <i>et al.</i> , 2009
86	<i>L. wuhuangmontis</i> Wang, Yang and Wang, 2018	Wang <i>et al.</i> , 2018
87	<i>L. wulingensis</i> Qian, Xiao, Cao, Xiao and Yang, 2020	Qian <i>et al.</i> , 2020
88	<i>L. yae</i> Shi, Hou, Song, Jiang and Wang, 2021	Shi <i>et al.</i> , 2021
89	<i>L. yingjiangensis</i> (Yang, Zeng and Wang, 2018)	Yang <i>et al.</i> , 2018
90	<i>L. yunkaiensis</i> Wang, Li, Lyu and Wang, 2018	Wang <i>et al.</i> , 2018
91	<i>L. zhangyapingi</i> (Jiang, Yan, Suwannapoom, Chomdej and Che, 2013)	Jiang <i>et al.</i> , 2013

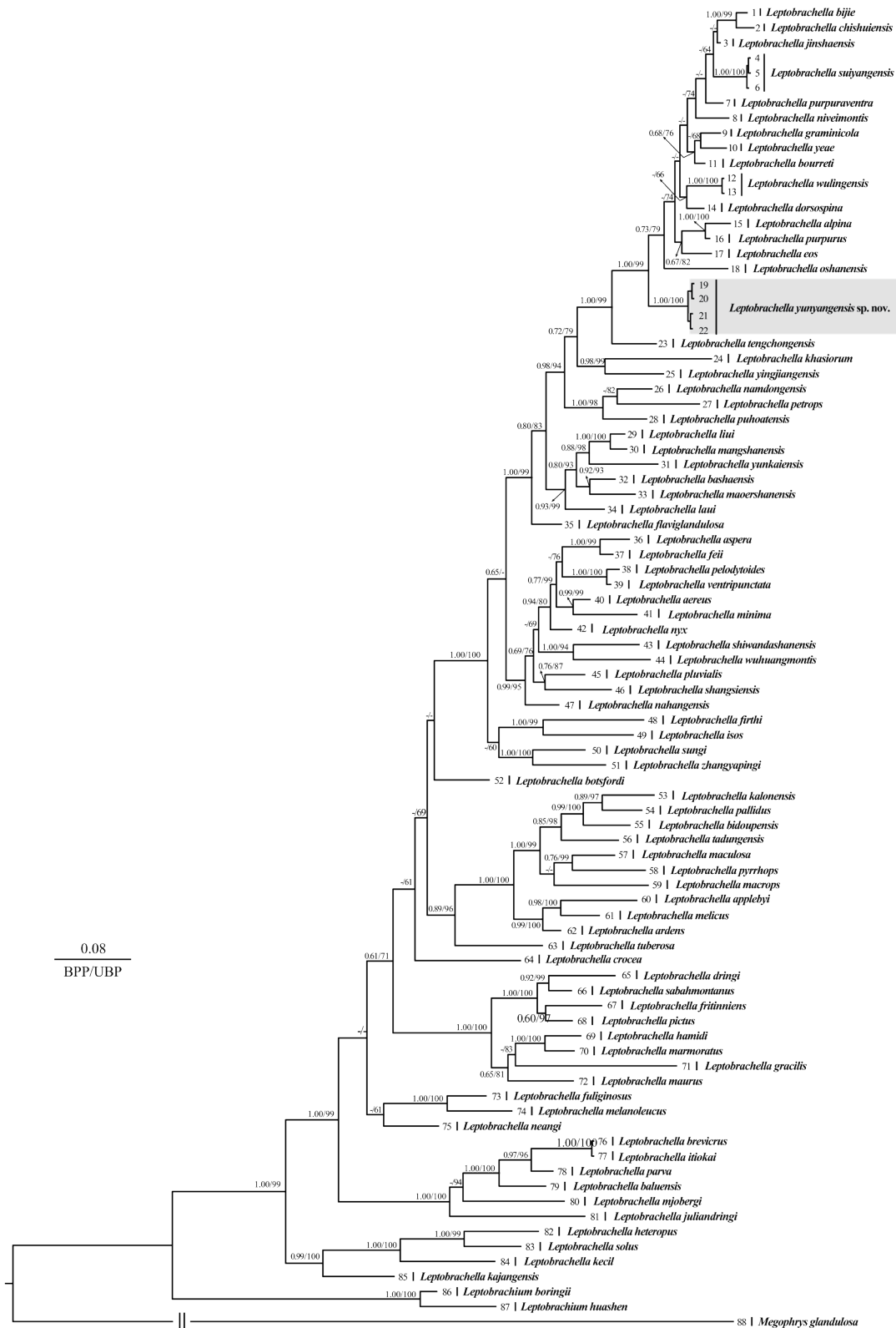


Figure 1 Bayesian inference (BI) tree based on mitochondrial 16S rRNA. In this phylogenetic tree, Bayesian posterior probabilities (BPP) from BI analyses/ultrafast bootstrap supports (UFB) from ML analyses are listed beside the nodes. The symbol “-” represents a value below 0.60/60. The scale bar represents 0.08 nucleotide substitutions per site. The numbers at the tips of branches correspond to the ID numbers in Table 1.

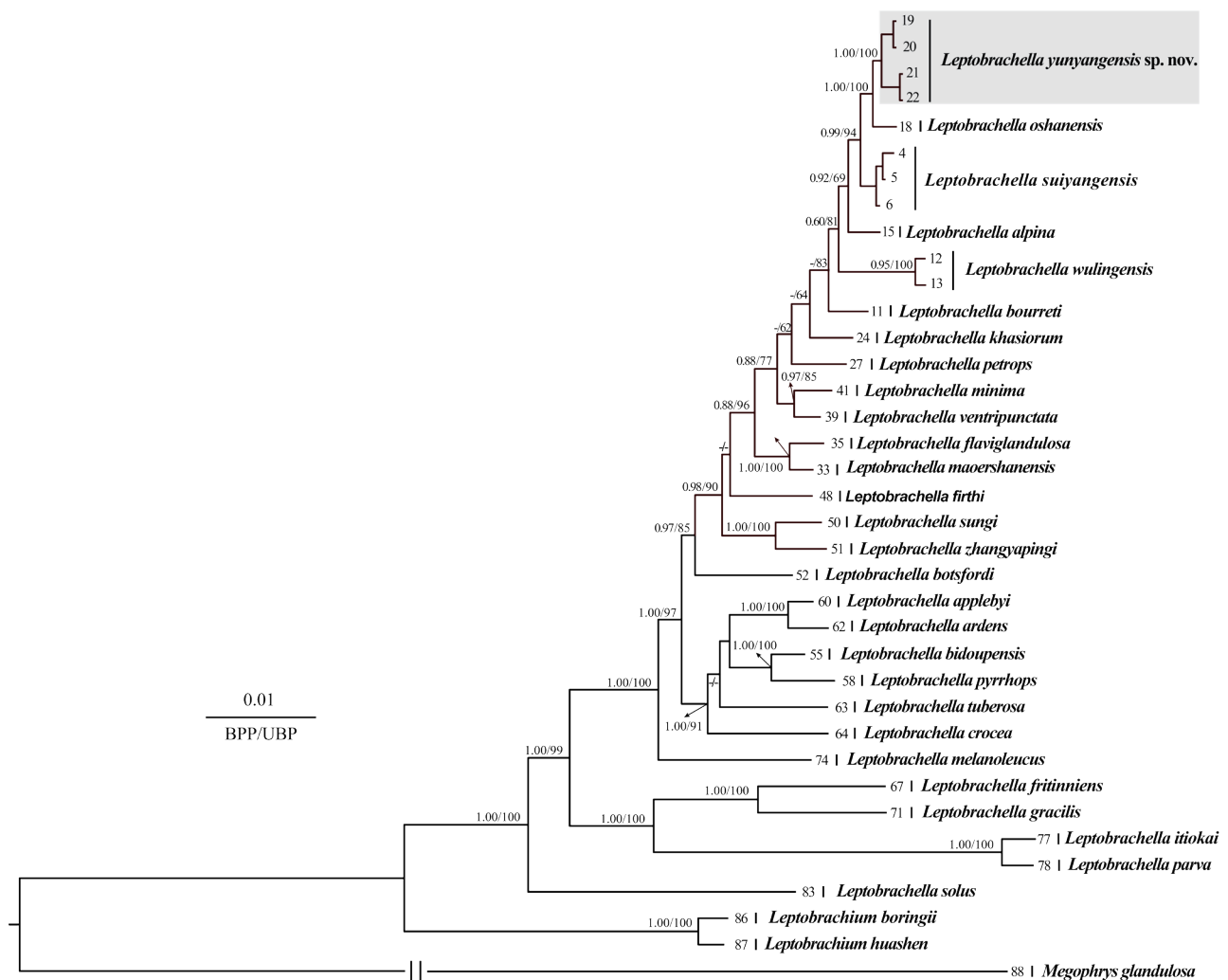


Figure 2 Bayesian inference (BI) tree based on combined nuclear data (six genes). BPP from BI analyses/UBP from ML analyses are listed beside the nodes. The symbol “-” represents values below 0.60/60. The scale bar represents 0.01 nucleotide substitutions per site. The numbers at the tips of branches correspond to the ID numbers in Table 1.

thighs are positioned at right angles to the body; (11) tibiotarsal articulation reaching to the anterior corner of the eye when the leg is stretched forward; (12) ventral surfaces of the throat, chest, and belly greyish white with purple-brown speckling; (13) lacking distinct blackish dorsolateral markings; and (14) transverse dark brown bars on the surfaces of limbs and digits.

Description of the holotype GZNU20210629001 (Figures 4 and 5), adult male. Body size moderate, SVL 30.6 mm.

Head length slightly wider than head width (HDL/HDW ratio: 1.13); snout short, rounded, and projecting beyond the lower jaw in dorsal view, longer than eye diameter (SNT/EYE ratio: 1.40); nostril rounded, distinct, and closer to the eye than tip of the snout (NEL/ SNT ratio: 0.45); canthus rostralis gently rounded; loreal region slightly concave; interorbital space flat and interorbital distance slightly longer than internarial distance

(IOD/IND ratio: 1.17); pineal ocellus absent; pupil vertical; eyes large, with eye diameter slightly equal to internarial distance (IND/EYE ratio: 1.00); tympanum distinct, rounded, and slightly concave, with a diameter smaller than that of the eye and larger than the tympanum-eye distance (TMP/EYE ratio: 0.51, TEY/TMP ratio: 0.78); upper margin of tympanum in contact with supratympanic ridge; distinct light-black supratympanic line present; vomerine teeth absent; vocal sac openings slit-like, paired, located posterolaterally on floor of the mouth in close proximity to the margins of the mandible; tongue cordiform, deeply notched behind; supratympanic ridge distinct, extending from posterior corner of the eye to the supra-axillary gland.

Forelimbs slender and comparatively short, length of lower arm and hand 47.06% of snout-vent length; tips of fingers rounded, slightly swollen; relative finger lengths I < II = IV < III;

Table 4 Morphological comparison of *Leptobrachella yunyangensis* **sp. nov.** (LY) and *L. oshanensis* (LO). All units in mm. The *P*-values were from Mann-Whitney *U* tests. The significance level was set at *P* < 0.05. Morphometric characters are explained in the Materials and Methods section.

Measurements	<i>Leptobrachella yunyangensis</i> sp. nov. Male (N=6)		<i>Leptobrachella oshanensis</i> * Male (N=11)		<i>P</i> -value <i>LY</i> vs. <i>LO</i>
	Range	Mean ± SD	Range	Mean ± SD	
SVL	27.9–30.6	29.3 ± 1.0	26.5–30.5	28.7 ± 1.4	0.301
HDL	9.1–11.6	10.7 ± 0.9	9.3–11.9	10.5 ± 0.7	0.591
HDW	9.6–10.6	10.1 ± 0.5	9.0–10.9	9.9 ± 0.6	0.733
SNT	4.2–4.9	4.5 ± 0.3	3.6–4.4	4.0 ± 0.3	0.005
EYE	3.1–3.7	3.5 ± 0.2	3.3–3.8	3.6 ± 0.2	0.256
IOD	3.3–4.1	3.6 ± 0.3	2.6–3.5	3.1 ± 0.2	0.001
IND	3.3–3.6	3.4 ± 0.1	2.5–3.3	2.9 ± 0.2	0.000
UEW	2.3–2.8	2.6 ± 0.2	2.2–2.8	2.6 ± 0.2	0.660
NEL	2.2–2.9	2.7 ± 0.3	1.9–2.8	2.3 ± 0.2	0.020
TMP	1.4–1.9	1.7 ± 0.2	1.6–2.1	1.9 ± 0.2	0.180
TEY	1.3–1.9	1.6 ± 0.3	1.0–1.5	1.3 ± 0.2	0.062
HND	7.1–7.7	7.4 ± 0.2	6.6–7.8	7.1 ± 0.4	0.078
LAHL	13.6–14.4	13.9 ± 0.3	12.4–14.6	13.8 ± 0.8	0.591
LW	1.2–2.5	1.6 ± 0.5	1.8–2.5	2.2 ± 0.2	0.015
HLL	42.6–49.8	47.2 ± 2.8	41.9–51.0	46.9 ± 2.7	0.884
THL	12.3–13.8	12.6 ± 0.6	11.9–14.3	13.2 ± 0.8	0.180
TIB	13.8–15.3	14.7 ± 0.6	11.8–14.8	13.6 ± 0.9	0.020
TW	4.1–4.8	4.4 ± 0.2	3.0–3.7	3.4 ± 0.2	0.000
FOT	13.2–13.9	13.6 ± 0.2	11.4–14.6	12.6 ± 0.9	0.015
TFL	18.6–20.8	19.8 ± 0.8	18.2–22.0	20.1 ± 1.2	0.591
HDL/HDW	0.95–1.13	1.06 ± 0.06	0.99–1.14	1.06 ± 0.06	1.000
HDL/SVL	0.32–0.39	0.36 ± 0.02	0.35–0.39	0.37 ± 0.02	1.000
SNT/HDL	0.36–0.47	0.43 ± 0.04	0.35–0.42	0.38 ± 0.02	0.020
SNT/EYE	1.16–1.55	1.32 ± 0.14	1.04–1.25	1.12 ± 0.07	0.002
EYE/TMP	1.84–2.21	2.01 ± 0.16	1.65–2.13	1.91 ± 0.17	0.301
EYE/HDL	0.29–0.36	0.33 ± 0.03	0.30–0.38	0.34 ± 0.03	0.180
EYE/UEW	1.22–1.46	1.36 ± 0.08	1.21–1.50	1.39 ± 0.08	0.462
IOD/UEW	1.18–1.71	1.42 ± 0.21	1.11–1.31	1.20 ± 0.06	0.015
IOD/IND	0.94–1.17	1.05 ± 0.08	0.91–1.15	1.07 ± 0.07	0.462
TIB/SVL	0.49–0.52	0.50 ± 0.01	0.45–0.50	0.48 ± 0.01	0.001
LAHL/SVL	0.46–0.49	0.47 ± 0.01	0.47–0.50	0.48 ± 0.01	0.149
HLL/SVL	1.53–1.76	1.61 ± 0.09	1.58–1.69	1.63 ± 0.03	0.301
TIB/HLL	0.28–0.34	0.31 ± 0.02	0.28–0.29	0.29 ± 0.00	0.027

Note : * Morphological data from Shi *et al.* (2021).

nuptial pad absent; subarticular tubercles absent; inner palmar tubercle large, rounded, and separated from the smaller, round outer palmar tubercle; inner metacarpal tubercles longer than outer metacarpal tubercles (IPTL/OTPL ratio: 1.67); absence of webbing and lateral fringes on fingers.

Hindlimbs slender, tibia slightly longer than thigh length

(TIB/THL ratio: 1.10) and 45.10% of snout-vent length; heels overlapping when thighs are positioned at right angles to the body; relative toe length I < II < V < III < IV; tips of toes round and slightly swollen; subarticular tubercles absent; toe webbing rudimentary; narrow lateral fringes present on all toes; inner metatarsal tubercle present and large, oval, outer metatarsal

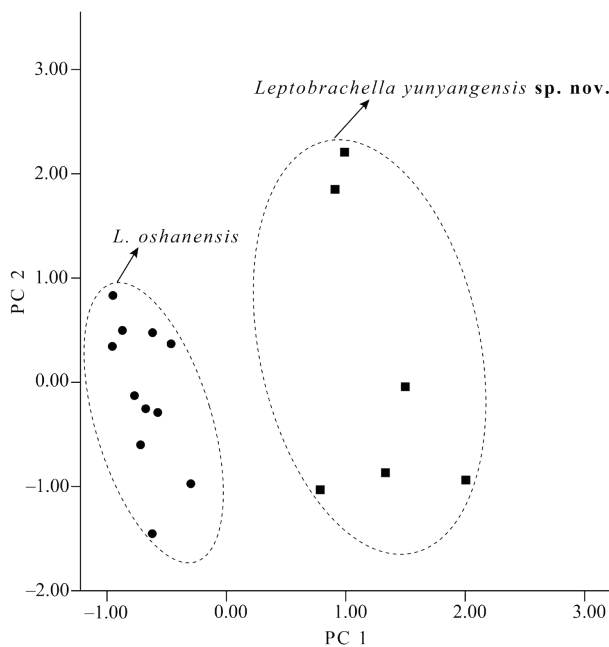


Figure 3 Plots of the first principal component (PC1) versus the second (PC2) for *Leptobrachella yunyangensis* sp. nov. and *L. oshanensis* from a principal component analysis.

tubercle absent; tibiotarsal articulation reaching to anterior corner of the eye when the leg is stretched forward.

Dorsal skin rough, with sparse large granules and tubercles; short longitudinal ridges on the shoulder; conical spines on the flanks; ventral skin smooth; pectoral gland and femoral gland milky-white, distinctly visible, and oval; long longitudinal skin ridges on dorsal surface of the limbs; dense tiny granules present on ventral surface of thigh and tibia; femoral gland situated on posteroventral surface of the thigh, closer to knee than to vent, oval; supra-axillary glands long, oval, and raised; ventrolateral glands distinctly visible and raised, forming an incomplete line.

Coloration of holotype in life (Figure 4) Dorsum greyish brown, with distinct darker brown markings on sides and scattered with irregular light greyish brown pigmentation and yellowish brown spots; a very indistinct, light brown inverted triangular pattern between the anterior corners of the eyes, without a dark brown W-shaped marking between the axillae; tympanum bicolored, with the upper 2/3 of the tympanum dark brown and the lower 1/3 light orange; light brown between the posterior corner of the eyes and the tympanum; sparse, small, light brown granules and small dark brown patches present on the dorsum of the body and limbs; transverse dark brown bars on dorsal surface of limbs and digits; distinct dark brown spots on the flanks from groin to axilla arranged longitudinally in two rows; elbow and upper arms with distinct light orange coloration; iris bicolored, with

the upper 1/3 of the iris copper orange and the lower 2/3 light silver gray.

Ventral surface of the throat, chest, and belly greyish white with purple-brown speckling; supra-axillary gland, femoral, pectoral, and ventrolateral glands white; ventral surface of limbs and lower lip dark grey-purple, scattered with small greyish white spots, creamy white tubercles, and small granules.

Coloration of holotype in preservation (Figure 5) Dorsum of body and limbs fade to dark brown except for upper arm; upper arm surface copper brown; skin on dorsal becoming more smooth; transverse bars on limbs becoming more distinct, and dorsolateral markings, longitudinal skin ridges and spots on back becoming indistinct. Ventral surface of limbs and surface of throat light brown, surface of abdomen greyish white, dark patches on chest, abdomen, and flanks becoming more distinct. Supra-axillary, femoral, pectoral, and ventrolateral glands greyish white.

Variation Measurements of the type series are shown in Table 2. All the male paratypes match the overall characters of the holotype, except that the ventral surface of the throat, chest, and belly is greyish brown in the holotype GZNU20210629001 (vs. light purple grey in the paratype GZNU20210622001) (Figure 6); tibiotarsal articulation with the same color as the thigh and tibia surfaces (vs. brown in the paratype GZNU20210622001); ventral surface of limbs dark purple grey (vs. violet blue in the paratype GZNU20210622001).

Sexual dimorphism Adult males with a comparatively large single subgular vocal sac, and absent nuptial pads and spines.

Comparison Comparative information on the new species with 63 recognized species of the genus *Leptobrachella* north of the Kra Isthmus is given in Table S4.

From the 26 known congeners of the genus *Leptobrachella* occurring south of the Kra Isthmus, by the presence of supra-axillary and ventrolateral glands, *Leptobrachella yunyangensis* sp. nov. can easily be distinguished from *L. arayai*, *L. dringi*, *L. fritinniens*, *L. gracilis*, *L. hamidi*, *L. heteropus*, *L. kajangensis*, *L. kecil*, *L. marmorata*, *L. melanoleuca*, *L. maura*, *L. picta*, *L. platycephala*, *L. sabahmontana*, and *L. sola* (vs. lacking supra-axillary and ventrolateral glands in the latter) by having a significantly larger body size (SVL 24.3–30.6 mm in males). *Leptobrachella yunyangensis* sp. nov. thus differs from the smaller *L. baluensis* (14.9–15.9 mm in males), *L. brevicrus* (17.1–17.8 mm in males), *L. bondangensis* (17.8 mm in a single adult male), *L. fusca* (16.3 mm in a single adult male), *L. itiokai* (15.2–16.7 mm in males), *L. juliandringi* (17.0–17.2 mm in males), *L. mjobergi* (15.7–19.0 mm in males), *L. natunae* (17.6 mm in a single adult male), *L. parva* (15.0–16.9 mm in males), *L. palmata* (14.4–16.8 mm in males), and *L. serasanae* (16.9 mm in a single adult female).

By the moderate body size of the male (SVL 28.3–30.6 mm), *Leptobrachella yunyangensis* sp. nov. differs from the larger *L.*



Figure 4 Morphological features of the live adult male holotype GZNU20210629001 of *Leptobrachella yunyangensis* **sp. nov.** A: dorsolateral view; B: dorsal view; C: ventral view; D: ventral view of the hand; E: ventral view of the foot. Photos A to E were taken at around 9:00 am.

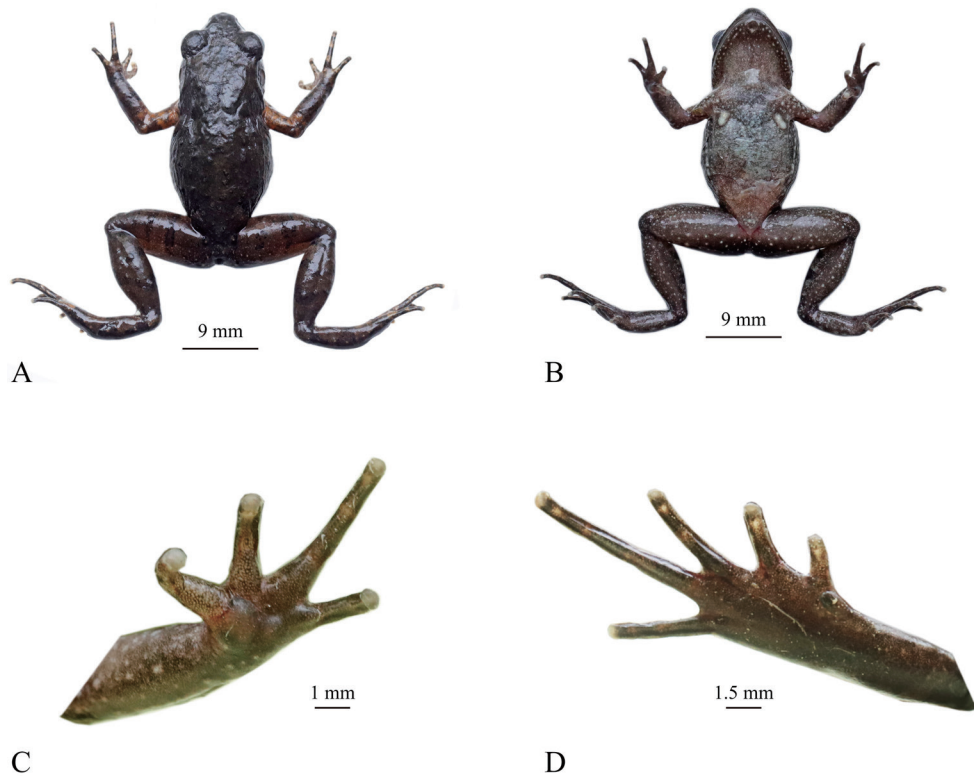


Figure 5 Morphological features of the preserved adult male holotype GZNU20210629001 of *Leptobrachella yunyangensis* **sp. nov.** A: dorsal view; B: ventral view; C: ventral view of hand; D: ventral view of foot.



Figure 6 Morphological features in life. *Leptobranchella yunyangensis* **sp. nov.**, paratype GZNU2021062200. A: dorsal view; B: dorsolateral view; C: ventral view; D: ventral view of the hand; E: ventral view of the foot. Photos A to E were taken at around 9:00 am.

damingshanensis (33.6–34.4 mm in males), *L. eos* (33.1–34.7 mm in males), *L. nahangensis* (40.8 mm in one male), *L. neangi* (35.4–36.3 mm in females), *L. sungi* (48.3–52.7 mm in males), *L. tamdil* (32.3 mm in one male), *L. zhangyapingi* (45.8–52.5 mm in males); from the smaller *L. alpina* (24.0–26.4 mm in males), *L. applebyi* (19.6–22.3 mm in males), *L. ardens* (21.3–24.7 mm in males), *L. aspera* (22.4 mm in one male), *L. bashaensis* (22.9–25.6 mm in males), *L. bidoupensis* (18.5–25.4 mm in males), *L. crocea* (22.2–27.3 mm in males), *L. feii* (21.5–22.8 mm in males), *L. flaviglandulosa* (23.0–27.0 mm in males), *L. graminicola* (23.1–24.6 mm in males), *L. isos* (23.7–27.9 mm in males), *L. khasiorum* (24.5–27.3 mm in males), *L. laui* (24.8–26.7 mm in males), *L. maculosa* (24.2–26.6 mm in males), *L. melica* (19.5–22.7 mm in males), *L. mangshanensis* (22.2–27.8 mm in males), *L. murphyi* (23.2–24.9 mm in males), *L. niveimontis* (22.5–23.6 mm in males), *L. pallida* (24.5–27.7 mm in males), *L. pluvialis* (21.3–22.3 mm in males), *L. rowleyae* (23.4–25.4 mm in males), and *L. tengchongensis* (23.9–26.0 mm in males).

For 15 species from the same lineage, i.e., *L. oshanensis*, *L. eos*, *L. purpurus*, *L. alpina*, *L. dorsospina*, *L. wulingensis*, *L. bourreti*, *L. yae*, *L. graminicola*, *L. niveimontis*, *L. purpuraventra*, *L. suiyangensis*, *L. jinshaensis*, *L. chishuiensis*, and *L. bijie*, *Leptobranchella yunyangensis* **sp. nov.** could be easily distinguished by several characters. The new species differs from *L. eos* (SVL 33.1–34.7 mm in males), *L. alpina* (SVL 24.0–26.4 mm in males), *L. graminicola* (SVL

23.1–24.6 mm in males), and *L. niveimontis* (SVL 22.5–23.6 mm in males) by moderate body size in the male (SVL 28.3–30.6 mm); from *L. eos* by the presence of black spots on the flanks (vs. their absence), narrow lateral fringes on the toes (vs. wide), and light grayish creamy white interspersed with light brown spots (vs. creamy white); from *L. oshanensis* and *L. jinshaensis* by rudimentary webbing on the toes (vs. lacking); from *L. purpurus* and *L. graminicola* by narrow lateral fringes on the toes (vs. wide) and indistinct dorsolateral markings (vs. distinct); from *L. dorsospina* by rough skin with sparse large warts and with short longitudinal ridges (vs. relatively smooth skin, some with small warts), indistinct dorsolateral markings (vs. distinct), and tibiotarsal articulation reaching to the anterior corner of the eye when the leg is stretched forward (vs. reaching to the posterior corner of the eye); from *L. wulingensis* by indistinct dorsolateral markings (vs. distinct), tibiotarsal articulation reaching to anterior corner of the eye when the leg is stretched forward (vs. reaching to the middle of the eye), and light grayish creamy white interspersed with light brown spots (vs. creamy white with distinct or indistinct brown speckling at margins); from *L. bourreti* and *L. yae* by rough skin with sparse large warts and with short longitudinal ridges (vs. relatively smooth skin) and indistinct dorsolateral markings (vs. distinct); from *L. purpuraventra*, *L. suiyangensis*, *L. chishuiensis*, and *L. bijie*

by indistinct dorsolateral markings (vs. distinct), tibiotarsal articulation reaching to anterior corner of the eye when the leg is stretched forward (vs. reaching to the middle of the eye or reaching the tympanum).

Leptobrachella yunyangensis **sp. nov.** differs from *L. aerea*, *L. botsfordi*, *L. crocea*, *L. isos*, *L. pallida*, *L. petrops*, *L. tuberosa*, and *L. zhangyapingi* by the presence of black spots on flanks (vs. absent in the latter).

Leptobrachella yunyangensis **sp. nov.** differs from *L. ardens*, *L. kalonensis*, *L. shiwandashanensis*, and *L. tadungensis* by rudimentary webbing on toes (vs. lacking toe webbing in the latter) and from *L. pelodytoides*, *L. sungi*, and *L. tamdil* (vs. wide toe webbing in the latter).

Leptobrachella yunyangensis **sp. nov.** differs from *L. lateralis*, *L. macrops*, *L. minima*, *L. namdongensis*, *L. nyx*, *L. pyrrhops*, and *L. ventripunctata* by narrow lateral fringes on toes (vs. lacking in the latter) and from *L. murphyi*, *L. yingjiangensis* and *L. yunkaiensis* (vs. wide lateral fringes in the latter).

Leptobrachella yunyangensis **sp. nov.** differs from *L. applebyi*, *L. ardens*, *L. bidoupensis*, *L. kalonensis*, *L. melica*, *L. minima*, *L. nahangensis*, *L. namdongensis*, *L. shangsiensis*, and *L. tadungensis* by the dorsal skin being rough with numerous tubercles and short longitudinal ridges (vs. dorsum smooth); from *L. bourreti* (vs. dorsum relatively smooth with small warts), *L. fuliginosa* (vs. dorsum smooth with fine tubercles), *L. mangshanensis* (vs. dorsum nearly smooth), *L. nokrekensis* (vs. dorsum tubercles and longitudinal folds), and *L. pelodytoides* (vs. dorsum with small, smooth warts).

Leptobrachella yunyangensis **sp. nov.** differs from *L. damingshanensis*, *L. dorsospina*, *L. maoershanensis*, *L. puhoatensis*, *L. purpuraventra*, *L. wuhuangmontis*, and *L. wulingensis* by lacking distinct blackish dorsolateral markings (vs. distinct blackish dorsolateral markings in the latter).

Currently, only one species of the genus *Leptobrachella*, namely, *L. oshanensis*, is distributed in Chongqing City, China, and this species can be distinguished by a combination of the following morphological characters. *Leptobrachella yunyangensis* **sp. nov.** differs from *L. oshanensis* by having rudimentary webbing and narrow lateral fringes on the toes (vs. lacking), dorsal skin shagreened with numerous tubercles and short longitudinal ridges (vs. dorsum smooth with few glandular ridges), tibiotarsal articulation reaching to anterior corner of the eye when the leg is stretched forward (vs. reaching to the middle of the eye), and lacking distinct blackish dorsolateral markings (vs. distinct blackish dorsolateral markings). The mean values of SNT, IOD, IND, NEL, TIB, TW, FOT are significantly greater than those of *L. oshanensis* for males of the new species (Table 4). In addition, in males the mean values of SNT/HDL, SNT/EYE, IOD/UEW, TIB/SVL, and TIB/HLL were significantly larger in *Leptobrachella yunyangensis* **sp. nov.** than in *L. oshanensis*

(*P*-values < 0.05; Table 4).

Distribution and ecology *Leptobrachella yunyangensis* **sp. nov.** is only known from the type locality of Lianhua Village, Renhe Town, Yunyang County, Chongqing, China and Qiyaoshan Nature Reserve, Chongqing, China, at elevations of 947–1200 m. Individuals of this new species are mostly found in grasses and shrubs near streams. In areas where the new species was found, *Leptobrachella yunyangensis* **sp. nov.** is sympatric with *Panophrys baolongensis* (Ye, Fei and Xie, 2007), *Rana omeimontis* (Ye and Fei, 1993), *Odorrana hejiangensis* (Deng and Yu, 1992), *Polypedates braueri* (Vogt, 1911), *Hyla annectans* (Jerdon, 1870), and *Fejervarya multistriata* (Hallowell, 1860). These species were often found in the same streams as *Leptobrachella yunyangensis* **sp. nov.** Males were not heard calling during the field survey from June 20 to 29, 2021.

4. Discussion

Phylogenetic analyses based on mitochondrial 16S rRNA and six nuclear genes suggested that the specimens collected in this study belonged to the genus *Leptobrachella* but were distinct from all previously described species for the molecular marker mitochondrial 16S rRNA, the minimum distance between *Leptobrachella yunyangensis* **sp. nov.** and its congeners was 4.8% (vs. *L. bourreti*), greater than the current threshold of 3.0% difference between amphibian species (Fouquet *et al.*, 2007). In fact, this is much greater than the genetic divergence between the recognized species of the genus *Leptobrachella* (Table S2). Morphologically, *Leptobrachella yunyangensis* **sp. nov.** has a number of features to distinguish it from congeners; for example, the presence of supra-axillary and ventrolateral glands, medium body size, the presence of black spots on the flanks, lacking distinct dorsolateral markings, and narrow lateral fringes on the toes (see the Comparison section for details). Thus, the combined morphological and genetic divergence data support the validity of *Leptobrachella yunyangensis* **sp. nov.** as a new species.

In the past decade, 24 new species of the genus *Leptobrachella* have been discovered in southern China (Sung *et al.*, 2014; Yang *et al.*, 2016; Yuan *et al.*, 2017; Yang *et al.*, 2018; Wang *et al.*, 2018; Hou *et al.*, 2018; Chen *et al.*, 2019; Wang *et al.*, 2019; Wang *et al.*, 2020; Chen *et al.*, 2020; Li *et al.*, 2020; Luo *et al.*, 2020; Lyu *et al.*, 2020; Qian *et al.*, 2020; Chen *et al.*, 2021a, b; Cheng *et al.*, 2021; Shi *et al.*, 2021), and the discovery of these new species has deepened our understanding of their diversity and evolutionary history. The work of Chen *et al.* (2018) provides a good framework for the phylogenetic study of the genus *Leptobrachella*. Unfortunately, this large-scale phylogenetic study included only one sample from Nanchuan, Chongqing, China, and the limited sample size may have led to an underestimation of species diversity.

The discovery site of *Leptobrachella yunyangensis* **sp. nov.** is located in the transition zone of biodiversity extending from the mountains of southwest China to the Qinba Mountains, and the discovery of the new species provides important additional material for understanding the detailed evolutionary history and biogeographic patterns of the genus. The continued field surveys are important for understanding and conserving the biodiversity of the region. In addition, because this group is highly dependent on forest habitat and is temperature sensitive, it is particularly important to protect its macroecology-dependent microhabitats. Therefore, in the context of global warming, there is an urgent need for a comprehensive, systematic, and in-depth survey of the impacts of climate change on terrestrial vertebrates to provide a basis for rational decisions regarding amphibian conservation (IPCC, 2014).

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Appendix

Specimens examined

Leptobranchella alpina (N=5): China: Yunnan Province: Jingdong County: Mt. Wuliang (type locality): GZNU20160623002–623006.

Leptobranchella suiyangensis (N=8): China: Guizhou Province: Suiyang County: Huoqiuba Nature Reserve (type locality):

GZNU20180606007 (holotype), GZNU20180606001–606006, GZNU20180606008.

Leptobranchella wulingensis (N=2): China: Guizhou Province: Shibing County: Mt. Yuntai (topotype locality): GZNU20170501, GZNU20170503.

Table S1 Primers used in PCR and sequencing in this study.

Locus	Primer Name	Primer Sequence	Annealing Temperature (°C)	Reference
16S	L3975	CGCCTGTTTACCAAAAACAT	55	Simon <i>et al.</i> (1994)
	H4551	CCGGTCTGAACCTCAGATCACGT		
BDNF	BDNF-F	ACCATCCTTTTCCTKACTATGG	53	Vieite <i>et al.</i> (2007)
	BDNF-R	CTATCTTCCCCTTTTAATGGTC		
RAG1	RAG1_F	AGCTGCAGYCARTACCAYAAATGTA	60	Mauro <i>et al.</i> (2004) Fu <i>et al.</i> (2007)
	RAG1_R	GCAAAGTTTCCGTTTCATTCTCAT		
RHOD	RHOD_F	ACCATGAACGGAACAGAAGGYCC	59	Frost <i>et al.</i> (2006)
	RHOD_R	CCAAGGGTAGCGAAGAARCCTTC		
NCX	NCX_1F	ACAACAGTRAGRATATGGAA	50	Shimada <i>et al.</i> (2011)
	NCX_1R	CCTTCTGTTTCRATGATCAT		
NTF3	NTF3_F	TCTTCCTTATCTTTGTGGCATCCACGCTA	57	Santos and Cannatella (2011)
	NTF3_R	ACATTGRGAATTCCAGTGTGTGTCGTCA		
SLC8A3	SCF_1F	CCATAGARGTCATAACATCACA	50	Shimada <i>et al.</i> (2011)
	SCF_1R	TTCATRACYTTGCCRTCCAT		

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Table S2 Uncorrected *P*-distance between *Leptobrachella* species for the 16S rRNA gene sequences.

ID	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42									
1	<i>L. yungangensis</i> sp. nov.																																																			
2	<i>L. suiyoungensis</i>	7																																																		
3	<i>L. aerea</i>	9.9	10.9																																																	
4	<i>L. alpina</i>	6.1	4.8	9.3																																																
5	<i>L. applebyi</i>	15	13.7	14.1	15.7																																															
6	<i>L. bialensis</i>	17.6	16.3	16.3	16.9	14.4																																														
7	<i>L. bidoupensis</i>	14.1	14.1	12.5	14.1	10.5	14.7																																													
8	<i>L. bijie</i>	6.4	4.5	10.2	6.4	15.3	18.8	15.3																																												
9	<i>L. bosfordi</i>	13.7	13.1	9.9	13.1	12.5	14.7	10.9	13.7																																											
10	<i>L. bourreti</i>	4.8	2.9	9.9	4.2	14.4	16.3	14.1	4.8	12.8																																										
11	<i>L. brevicus</i>	19.2	17.9	17.9	18.2	15.7	9.6	16.3	19.5	17.6	18.5																																									
12	<i>L. dringi</i>	16	15.7	15.3	15.7	14.4	15.7	14.7	17.6	12.5	16	17.3																																								
13	<i>L. eos</i>	5.8	5.4	11.2	4.5	16	17.6	14.1	6.4	11.5	3.5	19.8	16																																							
14	<i>L. firih</i>	12.5	13.4	11.5	11.8	16.6	17.6	14.7	14.4	12.5	11.8	18.2	16	12.5																																						
15	<i>L. fritimens</i>	15	16.3	14.4	15	15.3	16.6	14.7	17.9	11.8	16.6	18.2	8.6	16.3	15																																					
16	<i>L. gracilis</i>	20.1	18.5	17.9	19.5	17.6	18.8	18.5	20.8	16.9	19.5	20.4	13.7	20.1	20.1	14.1																																				
17	<i>L. hamidi</i>	14.1	15	14.1	15	15	15.7	14.7	17.3	13.1	16	17.6	10.2	14.7	16	7.7	12.1																																			
18	<i>L. heteropus</i>	19.2	20.4	16.9	20.1	16.9	18.2	16	21.1	18.2	19.2	20.1	17.9	19.8	20.4	18.8	20.1	16.9																																		
19	<i>L. issos</i>	10.9	11.8	11.5	10.5	13.7	16	11.8	13.1	12.1	9.6	18.2	15.7	11.2	10.9	14.7	18.8	13.7	18.2																																	
20	<i>L. tiakui</i>	19.2	17.9	17.9	18.2	15.7	9.6	16.3	19.5	17.6	18.5	0	17.3	19.8	18.2	18.2	20.4	17.6	20.1	18.2																																
21	<i>L. juliaudringi</i>	17.9	16.3	17.9	17.3	16.6	12.8	15.7	18.2	16.3	16.9	13.7	18.8	17.6	19.8	19.8	18.8	16.9	18.5	19.5	13.7																															
22	<i>L. kaogensis</i>	16.9	15.7	12.5	16.6	13.1	16.9	12.8	17.6	12.8	15	17.6	16.6	16.9	16.6	14.7	15.7	14.1	14.4	13.7	17.6	17.6																														
23	<i>L. kecil</i>	20.4	17.3	17.6	17.3	17.6	19.2	17.9	20.8	18.5	17.3	21.7	19.8	18.8	22.4	20.8	21.7	20.1	11.8	18.2	21.7	19.2	13.4																													
24	<i>L. khsiorum</i>	12.8	13.4	13.7	13.1	16.9	16.9	14.4	14.1	11.8	11.8	19.5	16	11.2	13.1	18.2	19.5	15.7	17.9	14.7	19.5	18.8	17.6	19.2																												
25	<i>L. lui</i>	8.3	10.9	8	8.9	15.7	16	12.1	10.2	10.5	8	18.8	15.7	8	11.5	16.3	22.4	16.3	19.5	10.9	18.8	19.5	15.7	19.2	9.6																											
26	<i>L. laui</i>	9.3	11.2	8.9	9.3	14.7	17.9	14.7	10.2	11.2	9.6	19.5	15	9.6	11.5	16.9	19.5	15.3	19.8	11.2	19.5	18.8	16.6	20.4	10.5	6.1																										
27	<i>L. macrops</i>	14.1	14.7	12.5	14.4	11.5	16	7.7	16.9	13.1	14.1	17.9	14.7	15	15.3	14.4	17.3	13.7	18.8	13.4	17.9	18.5	14.7	20.4	16.3	12.8	15																									
28	<i>L. mangshanensis</i>	9.3	11.2	8.3	8.9	15.3	16	12.5	10.5	10.9	8.9	18.5	16	9.6	12.1	16.3	22.4	16.3	19.2	11.5	18.5	18.8	16	19.5	10.5	1.9	6.1	13.1																								
29	<i>L. maoshanensis</i>	9.6	11.5	7.3	10.9	15.7	16.3	12.5	12.1	11.2	9.3	18.8	16.3	10.5	14.1	16.6	22	15.3	18.5	11.5	18.8	19.2	15	18.5	12.1	5.1	7.3	13.4	4.8																							
30	<i>L. marmorata</i>	14.7	14.4	14.1	14.7	13.1	14.7	14.4	16	11.5	15	16.3	9.6	14.4	14.4	8	12.5	4.5	17.6	14.1	16.3	16.9	13.1	20.8	14.7	15	15.3	13.4	15	15																						
31	<i>L. maura</i>	13.7	12.8	12.5	12.8	14.1	15.7	15	14.1	13.1	13.4	16	10.9	15	15.3	11.2	13.1	8.3	18.5	13.1	16	18.5	11.8	17.6	14.4	15.7	15.3	14.7	16	15	8.3																					
32	<i>L. melanoleucus</i>	13.1	13.4	13.4	13.1	14.4	16.6	13.1	14.1	12.1	13.1	17.3	15	13.4	16.6	15	17.3	16	18.2	15.7	17.3	15	15	17.3	13.7	14.7	16	13.7	14.4	14.7	15	13.7																				
33	<i>L. medica</i>	13.1	12.1	10.2	12.8	7.7	13.4	8.6	13.7	11.5	12.1	16	14.7	14.1	14.7	14.4	16.6	13.1	16	13.7	16	14.1	12.8	16.9	15	14.4	14.7	10.2	14.7	14.4	12.8	12.8																				
34	<i>L. minimus</i>	11.8	13.1	5.4	11.2	16.3	17.6	14.1	12.1	10.9	11.5	19.2	16	11.5	12.5	14.7	17.9	15.7	17.9	12.5	19.2	19.2	15.3	19.8	12.8	10.2	10.2	14.1	9.6	9.3	15	14.1	13.7	12.5																		
35	<i>L. mjobergi</i>	19.2	16.9	15.7	18.5	17.6	10.9	15.3	18.8	12.5	17.6	14.7	16.6	17.3	16.6	16.9	19.2	15.7	18.8	16.9	14.7	14.1	14.7	19.8	18.2	17.9	17.9	17.6	17.6	17.3	14.7	16.9	17.9	15	16.9																	
36	<i>L. nahangensis</i>	10.5	10.9	4.8	10.2	14.1	15.7	11.8	11.2	8	9.3	16.6	13.4	10.2	8.9	14.4	17.3	13.1	16.6	9.6	16.6	16.9	13.4	17.3	11.5	8	8.9	12.1	8.6	8.9	12.1	12.1	12.5	10.2	5.8	15																
37	<i>L. nyx</i>	9.3	10.5	3.5	8.9	14.1	16	11.8	9.9	9.3	9.6	17.3	14.7	9.6	10.2	13.7	19.5	14.1	16.6	11.2	17.3	17.6	13.7	18.2	13.1	7.3	8.6	13.1	7.7	8	13.1	13.4	13.1	10.2	6.4	16.3	3.8															
38	<i>L. oshanensis</i>	5.4	6.7	10.2	6.4	14.7	16.9	14.1	7.3	11.8	5.1	17.9	16.6	5.4	12.5	15.7	20.8	15	19.8	11.8	17.9	16.6	16.3	19.2	12.5	7.3	9.6	14.4	8.3	9.3	14.1	15	13.7	12.8	11.5	17.3	10.2	9.6														
39	<i>L. pallida</i>	14.4	13.4	11.8	13.7	10.2	15.3	6.7	15	11.2	14.4	15.7	13.7	13.7	15.3	14.7	16.9	13.4	17.9	14.4	15.7	14.1	18.8	15.3	12.8	13.7	8.6	13.1	13.7	12.8	13.7	13.7	10.2	13.4	15.7	11.5	11.8	12.8														
40	<i>L. parva</i>	18.5	16.6	16.6	17.9	14.7	6.1	15.3	18.8	15	17.3	5.4	16	18.5	17.3	16.6	18.8	16	19.2	15.3	5.4	14.1	15.3	19.8	18.5	16.3	18.2	16.3																								

Continued Table S2

ID	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	
42	<i>L. picta</i>	15	15.7	15.3	15.3	15.7	15.7	15.3	17.6	13.4	16	17.6	6.7	16.3	14.4	5.8	12.8	9.6	18.2	16	17.6	19.8	16.9	20.8	16.3	16.6	16.9	14.7	16.6	16.9	8.6	10.5	15.3	14.7	15.3	17.6	14.1	14.7	15.7	14.7	16	16		
43	<i>L. pluvialis</i>	9.9	10.9	4.8	9.6	14.1	16	12.8	11.5	10.2	8.9	17.3	15	9.9	11.5	15.3	19.8	15.3	16.9	11.8	17.3	17.6	14.7	17.9	12.1	7	8.3	13.1	7.3	6.4	14.4	14.7	12.8	11.8	6.4	17.3	4.8	4.5	9.3	12.5	16	10.5	15.7	
44	<i>L. pulchra</i>	11.8	11.5	10.9	10.5	15.3	16.6	14.1	11.8	9.3	10.2	17.3	15.7	11.2	12.1	16.3	20.4	15.7	19.2	11.8	17.3	19.2	16	19.5	10.9	9.6	9.6	14.4	9.6	10.5	14.1	12.8	14.4	13.4	10.5	16.9	8	9.6	10.9	15	16.9	7	15.7	
45	<i>L. purpurea</i>	5.4	3.8	9.3	1.9	15	16.6	12.8	5.4	12.1	3.2	18.5	16	2.6	12.1	15.7	20.1	14.7	19.8	10.5	18.5	16.6	16.3	17.9	12.1	8	8.9	14.1	8	9.6	13.7	13.7	13.4	12.8	11.2	17.3	10.2	8.3	5.1	12.8	17.6	11.5	15.7	
46	<i>L. purpuraventria</i>	6.1	3.5	9.9	5.4	14.1	16.9	14.4	4.2	12.5	2.6	18.5	16.6	4.5	13.7	16.6	19.8	15.3	19.2	11.5	18.5	17.6	15	16.9	13.1	9.3	10.9	14.4	10.2	9.9	14.1	13.4	13.1	11.2	11.5	17.3	9.9	9.6	5.1	13.7	17.3	12.1	16.3	
47	<i>L. pyrrhops</i>	15	14.1	11.5	14.4	12.8	14.4	8.3	16.3	10.9	13.7	17.6	14.7	13.7	15	14.4	15.3	14.7	16.3	13.1	17.6	16	11.5	17.3	15	13.1	13.7	8	13.4	13.1	14.4	15	14.4	11.2	12.1	13.4	11.5	12.1	14.4	7.3	15.3	13.1	14.7	
48	<i>L. sabahmontana</i>	15.7	16	14.7	15	14.4	15.7	14.1	17.9	12.1	16	16.6	6.7	15.7	14.7	6.4	13.4	8.6	19.5	15.3	16.6	18.5	15.7	20.4	16	16	16	13.4	16	16.3	8.3	8.6	14.1	12.8	14.4	16.6	12.8	14.1	16	12.8	15.3	15.3	4.8	
49	<i>L. shangensis</i>	11.8	12.5	6.7	11.2	16	17.9	14.7	12.1	11.2	10.9	19.2	16.6	10.9	13.1	15	19.5	15	18.5	13.1	19.2	17.9	16.6	20.8	14.4	9.3	9.6	14.1	8.9	9.3	14.7	16	14.4	13.1	7	18.2	6.4	6.1	10.2	13.7	17.9	13.7	16.6	
50	<i>L. solus</i>	20.1	18.8	16.3	19.2	18.2	17.9	17.9	20.4	17.9	18.2	19.5	18.5	19.2	20.4	19.2	19.5	18.2	7.7	18.2	19.5	11.2	10.2	20.4	19.2	20.8	18.8	19.2	19.2	17.9	16.9	19.8	18.2	18.8	17.6	16.3	17.6	19.5	17.6	16.6	20.8	17.6		
51	<i>L. sungi</i>	8.9	10.2	7.7	10.2	15	15.3	11.8	10.5	10.9	8	17.3	15.3	9.3	9.9	15	20.4	15.3	17.9	10.2	17.3	18.5	15.7	19.5	12.1	8.3	9.6	13.7	8.6	8.3	13.4	13.4	14.1	13.1	8.9	16.6	7	7.3	8.9	14.1	15.3	9.6	14.7	
52	<i>L. tengchongensis</i>	7.3	8.9	9.6	9.3	14.7	15.7	13.4	9.6	9.9	8	16.6	14.7	8	10.9	14.4	20.1	13.7	18.8	9.6	16.6	18.8	16.6	19.8	11.2	8	8.9	14.1	8.9	9.9	13.1	14.1	14.1	12.8	10.5	16.3	8.3	8.3	7	13.1	14.7	8	14.4	
53	<i>L. ventripunctata</i>	11.2	12.5	6.1	10.2	15.7	15.3	14.7	10.9	9.9	10.9	16.6	14.7	10.9	9.6	13.7	19.5	13.7	18.2	9.9	16.6	17.3	14.7	18.8	14.4	8.6	8.9	15	9.3	8.9	12.8	12.8	15	12.8	7.7	15.7	5.8	5.1	10.5	14.1	15.3	11.2	15	
54	<i>L. weihuangmontis</i>	12.8	13.1	8.6	11.2	15.3	16.9	13.1	13.1	12.5	10.9	18.8	17.6	11.5	12.8	16.3	20.1	16.3	17.9	11.2	18.8	18.8	14.1	18.2	14.1	10.5	12.5	14.4	9.9	10.2	14.7	15.3	13.7	13.1	8.9	17.9	8	8	12.8	14.4	18.2	14.4	17.6	
55	<i>L. yingjiangensis</i>	8.6	10.9	10.9	8.9	15.7	16.6	12.8	10.2	11.5	9.6	18.5	16.3	8.9	14.1	16.3	20.8	14.7	19.8	12.1	18.5	16.6	17.3	19.8	9.3	8	8.3	14.1	8.6	9.6	14.4	15	14.7	13.4	10.5	17.6	9.9	10.2	8.9	12.5	17.9	8.9	16.3	
56	<i>L. yunkaensis</i>	10.5	11.5	10.5	10.2	15.3	17.3	14.1	11.5	12.1	9.3	20.4	18.2	9.9	13.1	17.6	21.4	16.9	19.8	11.2	20.4	20.4	15.3	20.1	10.9	6.1	6.1	15.7	5.4	7	15.7	16	16.9	15.3	10.2	19.5	9.6	9.6	10.5	15	17.9	11.5	18.2	
57	<i>L. zhangyuping</i>	9.3	10.2	9.3	8.6	15.7	16.3	13.7	10.5	11.8	8.6	18.2	16.9	9.6	11.2	16.9	20.8	16.9	19.2	10.2	18.2	18.5	16.3	18.8	12.5	9.3	8.6	14.7	9.3	10.9	16	14.7	14.1	14.1	11.8	16.3	9.3	9.3	10.2	15	17.3	12.1	16.6	
58	<i>L. rivetmontis</i>	5.4	4.8	10.2	5.4	15.3	17.9	13.7	4.8	12.5	3.8	19.8	16.9	3.5	12.5	16.9	20.8	16	20.4	11.2	19.8	18.2	16	19.8	12.1	8	9.6	15.3	9.9	11.2	15	15.3	13.7	13.1	11.8	17.6	10.5	8	5.8	14.1	18.5	13.4	16.9	
59	<i>L. flaviglandulosa</i>	7.7	9.3	5.8	7.7	12.8	17.3	12.1	8	8.3	7.7	18.5	15	8.3	10.5	13.7	19.2	14.4	17.6	9.6	18.5	17.9	13.4	17.3	11.2	5.4	6.1	14.1	5.4	7.3	14.1	13.4	13.4	12.1	8.3	16.3	6.1	5.4	7.7	12.8	17.3	10.5	15.3	
60	<i>L. feii</i>	10.2	9.9	4.8	9.6	14.4	15.7	13.4	11.2	11.2	9.6	16	16.6	10.9	11.8	14.7	18.8	14.1	17.3	10.9	16	17.6	12.5	17.9	14.1	10.2	10.5	14.1	10.5	8.9	14.7	12.8	15.3	11.5	8.3	15.7	7.3	5.8	10.2	13.4	14.4	11.5	16.6	
61	<i>L. chishuensis</i>	6.1	4.2	9.3	5.8	15	18.5	15	1.9	12.5	3.8	19.8	16.9	6.1	13.7	17.6	21.1	16	19.5	12.8	19.8	17.3	16.9	19.2	12.8	9.3	9.6	16.6	9.6	10.5	15.7	13.1	13.7	12.5	12.1	18.8	9.9	8.9	7	15	19.5	12.5	17.3	
62	<i>L. nandongensis</i>	10.9	11.2	10.2	9.6	16.3	17.3	14.4	10.9	10.2	9.6	18.2	16	9.6	11.5	16.9	20.4	15.3	19.8	9.9	18.2	19.5	16	19.5	11.2	9.3	8	15	8.6	9.9	14.7	12.8	14.1	13.7	9.9	16.6	8.6	9.6	10.5	15.3	16.9	7.7	16	
63	<i>L. woltingensis</i>	5.1	4.5	8.9	5.1	14.4	16.6	14.1	5.1	11.5	2.2	19.2	15	3.8	12.1	15.7	19.5	14.4	18.5	9.6	19.2	16.6	15.7	17.9	11.5	7.7	8.6	14.7	8.6	8.9	13.4	13.4	13.7	12.1	10.2	17.3	7.7	8	5.4	14.1	17.9	11.2	15	
64	<i>L. fuliginosa</i>	14.7	14.4	12.5	13.4	17.6	13.1	15.3	10.9	13.1	19.2	15.3	13.7	17.3	14.1	16.9	15.7	16	13.4	19.2	15.7	13.7	15.7	13.7	14.7	15.3	14.4	14.4	14.4	14.4	14.4	14.4	14.4	14.4	14.4	14.4	14.4	14.4	14.4	14.4	14.4	14.4	14.4	14.4
65	<i>L. aspera</i>	10.2	11.2	5.1	10.2	14.7	16	13.7	12.1	9.6	9.6	17.3	16	10.2	11.5	14.1	18.8	13.4	17.3	10.2	17.3	13.4	18.2	12.8	9.6	9.9	14.4	9.9	8.3	14.1	13.4	15	11.5	6.7	15.3	7	6.1	10.2	14.4	15.7	10.5	16		
66	<i>L. dorsospina</i>	5.4	4.5	10.5	4.8	15.3	17.6	14.7	5.8	12.8	3.2	18.8	16	3.2	13.4	16	19.5	14.4	19.8	10.9	18.8	16.9	16.6	17.9	12.1	8.6	9.9	14.1	9.6	10.5	13.7	14.7	13.1	13.4	11.5	17.9	10.5	9.9	4.8	12.5	17.3	12.5	16	
67	<i>L. bashuensis</i>	8.3	9.6	7	8.3	12.5	15	12.5	9.6	9.9	7.3	16.6	14.4	8.6	11.8	14.7	18.8	13.7	17.3	9.6	16.6	17.6	12.8	17.3	10.9	6.1	5.8	13.4	5.1	5.1	12.5	12.5	14.1	12.8	8.9	15.7	8.3	7.3	8.3	13.7	14.7	10.2	14.7	
68	<i>L. jinshaensis</i>	5.8	2.6	10.2	4.8	15.3	18.5	15.3	2.6	13.4	2.9	18.8	16.6	3.8	13.7	16.9	19.8	16	21.1	11.5	18.8	17.6	16.6	19.5	13.4	9.6	9.9	15.7	10.5	11.5	15	14.1	13.1	13.4	11.8	18.5	10.5	9.3	5.4	14.4	18.2	12.8	16.9	
69	<i>L. neongi</i>	12.8	12.8	10.5	12.8	12.1	14.7	11.2	14.7	8	12.1	16.3	14.1	13.1	14.4	13.4	17.6	13.1	16.9	11.2	16.3	16.3	11.5	16	13.7	13.1	14.1	13.7	13.4	12.5	13.7	12.8	9.3	10.9	12.8	13.7	9.6	10.5	12.5	13.1	15	10.2	14.7	
70	<i>L. cracca</i>	14.7	13.7	11.2	14.7	13.7	14.4	10.9	14.1	9.3	13.4	16.6	12.1	14.1	14.4	14.1	15.3	13.1	17.3	13.1	16.6	16.9	11.8	17.6	12.1	13.7	13.7	13.1	14.7	13.4	12.8	11.5	13.7	11.8	13.7	13.7	10.9	12.5	15.3	11.5	15.7	13.4	13.4	
71	<i>L. tuberosa</i>	11.2	11.5	9.6	10.9	12.8	14.4	9.6	12.8	7.3	10.9	16.3	12.1	10.5	12.1	11.5	15	11.5	17.6	8.6	16.3	16.3	12.5	18.5	13.7	11.2	11.5	11.8	11.5	10.2	10.9	13.1	11.2	9.9	13.4	8	8	11.2	9.9	14.4	11.5	12.8		
72	<i>L. yue</i>	7	5.1	10.9	5.4	14.4	17.9	15.7	5.8	12.5	3.2	19.5	16.3	4.8	13.1	16.9	18.5	16	20.8	11.2	19.5	17.6	16.6	18.5	12.8	9.6	8.9	15	9.9	11.5	15.3	14.1	13.1	13.1	10.9	18.5	9.3	9.9	5.4	13.7	18.2	12.1	16.3	
73</																																												

Continued Table S2

ID	Species	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81		
42	<i>L. picta</i>																																									
43	<i>L. pluvialis</i>																																									
44	<i>L. pukoensis</i>	8.9																																								
45	<i>L. purpura</i>	8.9	10.5																																							
46	<i>L. purpuraventra</i>	9.3	9.9	4.2																																						
47	<i>L. pyrhopis</i>	12.1	14.1	13.4	13.7																																					
48	<i>L. sabahmontana</i>	15.7	15	15.3	16.6	13.7																																				
49	<i>L. shangensis</i>	5.4	10.5	10.5	10.9	13.1	15.3																																			
50	<i>L. solus</i>	18.2	20.8	19.2	18.5	15	18.5	20.1																																		
51	<i>L. sungi</i>	6.4	8	8.9	9.3	14.4	14.7	8.6	19.5																																	
52	<i>L. tengchongensis</i>	8.9	8.3	8.3	8	13.7	14.7	9.6	20.1	6.7																																
53	<i>L. ventripunctata</i>	6.4	8.9	10.2	10.2	12.5	13.4	7	18.5	7.3	8.6																															
54	<i>L. wuhuangmontis</i>	8.6	12.1	11.2	12.1	13.4	16	9.6	17.6	9.6	12.5	8.9																														
55	<i>L. yingjiangensis</i>	9.3	9.6	8	9.3	11.8	16	11.5	19.8	10.9	8.6	10.9	13.7																													
56	<i>L. yunkaiensis</i>	8.9	10.5	8.9	10.5	14.1	17.3	10.2	19.8	9.3	10.9	10.5	11.2	8.3																												
57	<i>L. zhongyuping</i>	8.6	10.9	8	10.2	14.1	16.3	10.5	19.8	6.7	8.3	9.6	12.1	11.2	11.2																											
58	<i>L. niueimontis</i>	9.6	11.8	3.5	5.1	15	17.3	11.5	20.1	9.6	8.3	10.9	12.5	9.9	10.2	9.9																										
59	<i>L. flaviglandulosa</i>	5.8	8.9	7	8.3	12.5	15	7	17.9	7.7	8	7	9.9	8	6.4	7.3	8																									
60	<i>L. fei</i>	6.1	10.9	8.9	10.2	13.1	16	8	17.6	8.3	9.3	7.3	9.6	11.5	11.8	8.9	9.9	8																								
61	<i>L. chishuensis</i>	9.9	10.2	5.1	3.2	16	17.3	10.9	19.5	10.5	9.3	10.2	12.5	9.9	10.2	10.2	5.1	7	10.9																							
62	<i>L. nandongensis</i>	9.9	5.1	8.9	9.6	14.4	15	11.2	20.1	8.3	8	8.3	12.8	9.3	8.9	9.9	10.2	8.3	11.2	9.9																						
63	<i>L. wulingensis</i>	8.6	8.9	4.2	3.5	13.7	15	9.9	17.6	8.3	7.7	9.3	10.5	8	8.6	10.2	4.8	6.7	9.9	3.5	9.3																					
64	<i>L. fuliginosa</i>	12.8	14.4	13.7	14.1	13.4	13.4	14.4	17.3	13.7	13.1	14.4	12.8	13.4	15.7	13.4	15.3	11.8	13.7	15	14.7	12.8																				
65	<i>L. aspera</i>	6.1	9.6	9.6	10.2	13.1	14.7	7	18.2	7.7	8.6	6.7	9.3	10.5	10.5	9.6	10.2	7.7	2.9	10.9	9.9	8.6	13.4																			
66	<i>L. dorsospina</i>	9.9	11.2	3.5	3.5	14.4	16.3	11.2	18.8	9.9	7	11.2	12.1	9.3	10.5	9.9	4.5	8.6	10.5	5.4	10.2	3.2	13.4	9.9																		
67	<i>L. bashuensis</i>	6.7	8.9	7	8.6	13.1	13.7	8.9	17.9	7.7	9.3	8.3	8.6	9.9	5.8	8.6	8.9	5.4	8	8.6	8.3	7.7	13.4	7.3	8.9																	
68	<i>L. jinshaensis</i>	10.5	10.9	3.5	2.9	15	16.9	11.2	19.2	10.2	8.3	10.5	12.5	9.6	10.9	10.5	2.9	8.6	9.9	2.9	9.9	3.2	14.1	10.5	3.2	9.6																
69	<i>L. nangi</i>	11.5	11.8	13.1	12.5	12.8	14.7	14.4	17.6	11.8	10.9	12.5	13.1	11.5	13.4	13.1	12.8	9.9	11.2	13.4	11.5	11.2	8.6	10.2	12.5	11.8	13.4															
70	<i>L. crocea</i>	12.1	12.8	14.1	14.1	12.5	12.8	15.3	15.7	13.1	13.7	12.8	14.4	11.8	15.3	14.4	13.4	12.1	12.5	13.7	12.8	13.4	12.8	12.1	15	11.5	14.7	10.9														
71	<i>L. tuberosa</i>	10.2	10.9	9.6	12.1	9.9	11.2	10.9	17.6	10.2	9.3	8.9	11.2	10.9	12.1	10.9	10.9	8.9	8.6	12.8	10.9	9.9	10.5	8.6	11.5	8.9	11.2	9.6	9.3													
72	<i>L. yue</i>	10.2	10.2	5.4	4.8	13.7	16	10.2	19.2	9.3	8.3	10.9	11.8	9.6	9.6	9.9	5.4	8	11.5	5.4	9.9	4.2	13.1	10.9	4.5	8.9	3.8	12.5	14.7	11.2												
73	<i>L. ardens</i>	11.8	13.4	12.8	11.8	7.7	13.7	12.8	16.9	13.4	13.1	12.8	12.1	12.8	15	13.4	13.7	11.8	11.8	13.4	14.4	12.1	11.8	12.5	12.8	10.9	13.7	9.9	11.2	10.2	12.1											
74	<i>L. kabonensis</i>	14.1	15.7	14.4	15.3	8.9	14.4	15	18.8	14.7	15	16	16	14.1	17.6	15.3	15	14.7	14.7	16.6	16.9	15.3	14.7	15.3	15.7	15	16	14.1	13.1	12.1	16.3	10.9										
75	<i>L. maculosa</i>	10.5	11.5	12.5	12.1	7	14.1	12.8	17.3	11.5	11.8	11.8	11.5	11.5	12.5	12.1	13.1	11.2	11.8	13.1	12.5	11.8	13.1	12.5	12.8	10.9	13.4	9.9	12.1	10.5	12.1	6.1	9.6									
76	<i>L. tudangensis</i>	11.8	13.1	12.8	14.4	7	13.1	13.4	17.3	12.8	13.1	13.1	13.7	12.1	13.1	14.4	13.7	10.5	12.8	14.4	13.4	13.1	12.5	12.8	14.7	12.1	14.1	11.2	11.2	9.3	14.1	7.7	7.3	6.7								
77	<i>L. pelodytoides</i>	6.1	9.3	10.2	10.9	12.5	13.4	7	18.5	7.3	8.6	0.6	8.9	10.5	10.5	9.6	10.9	7	7.3	10.9	8.9	9.3	14.1	6.7	11.2	8.3	11.2	12.5	12.5	8.9	10.9	12.8	16	11.8	13.1							
78	<i>L. graminicola</i>	9.9	10.2	4.8	4.2	14.7	15	11.5	18.5	8	8	10.9	10.9	9.9	9.3	9.9	4.8	8.3	10.9	4.8	9.6	2.6	13.4	9.6	4.2	8	3.8	12.1	13.1	10.9	3.5	13.1	15.7	12.8	13.4	10.9						
79	<i>L. shiwandashanensis</i>	8	9.6	11.2	11.5	14.7	15.3	8.9	21.1	8.9	10.9	9.9	8	12.5	11.8	11.8	12.5	10.2	7.3	12.1	11.2	11.5	15	7.3	12.5	8.6	12.5	13.7	13.7	12.1	12.1	13.4	17.3	12.8	14.1	9.9	11.2					
80	<i>L. huashen</i>	25.6	25.6	27.2	25.2	22.7	28.8	27.5	24.9	25.9	26.5	25.2	26.2	25.2	26.5	27.5	26.8	26.2	25.6	26.8	24.9	27.2	25.9	26.5	25.9	25.2	2															

Table S3 Variable loadings for principal components with eigenvalues greater than 1 from morphometric characters corrected by SVL.

Morphometric characters	PC 1	PC 2	PC 3
HDL	0.024	−0.5	0.497
HDW	0.091	−0.069	0.646
SNT	0.755	−0.054	−0.075
EYE	−0.508	0.244	0.602
IOD	0.741	0.024	−0.334
IND	0.743	0.183	0.234
UEW	−0.36	0.788	0.286
NEL	0.576	0.424	0.45
TMP	−0.424	−0.126	0.712
TEY	0.631	−0.425	0.226
HND	0.227	0.626	−0.064
LAHL	−0.513	0.739	−0.164
LW	−0.809	−0.25	−0.279
HLL	−0.279	0.361	−0.349
THL	−0.664	0.083	−0.061
TIB	0.605	0.496	0.052
TW	0.922	0.141	0.004
FOT	0.553	0.337	−0.039
TFL	−0.357	0.397	0.217
Eigenvalues	1.954	3.419	2.561
Percentage of total variance	31.175	15.908	12.245
Cumulative percentage	31.175	48.083	60.328

Table S4 Selected diagnostic characters for new species described herein and species in the genus *Leptobrachella* occurring north of the Isthmus of Kra (modified from Rowley *et al.*, 2017; Yuan *et al.*, 2017; Hou *et al.*, 2018; Wang *et al.*, 2018; Yang *et al.*, 2019; Hoang *et al.*, 2019; Chen *et al.*, 2020; Qian *et al.*, 2020). Grey shading indicates non-overlapping characters compared to *Leptobrachella yunyangensis* **sp. nov.**

ID	Species	Males SVL (mm)	Black spots on flanks	Toes webbing	Lateral fringes on toes	Dorsal skin texture	Distinct dorsolateral markings	Tibiotarsal articulation	Ventral coloration
1	<i>L. yunyangensis</i> sp. nov.	28.3–30.6	Present	Rudimentary	Narrow in males	Rough with sparse large warts, with short longitudinal ridges	No	Reaching to anterior corner of eye	Light grayish creamy white, interspersed with light brown spots
2	<i>L. aerea</i>	25.1–28.9	Absent	Rudimentary	Wide	Finely tuberculate	No	Reaching to tip of snout	Near immaculate creamy white, brown speckling on margins
3	<i>L. alpina</i>	24.0–26.4	Present	Rudimentary	Wide in males	Relatively smooth, some with small warts	Yes	Reaching to anterior corner of eye	Creamy-white with dark spots
4	<i>L. applebyi</i>	19.6–22.3	Present	Rudimentary	Absent	Smooth	Yes	Reaching to anterior corner of eye	Reddish brown with white speckling
5	<i>L. ardens</i>	21.3–24.7	Present	Absent	Absent	Smooth-finely shagreened	Yes	Reaching beyond tip of snout	Reddish brown with white speckling
6	<i>L. aspera</i>	22.4	Present	Rudimentary	Wide	Finely tuberculate	Yes	Reaching to anterior corner of eye	Near immaculate creamy white, brown speckles on margins
7	<i>L. bashaensis</i>	22.9–25.6	Present	Greatly reduced basal webbing	Narrow (only on II and III)	Lightly rough with small tubercles and irregular pustules	Yes	Reaching snout, well beyond anterior margin of eye, but not beyond snout tip	Belly off-white, with faint spots
8	<i>L. bidoupensis</i>	18.5–25.4	Present	Rudimentary	Narrow	Smooth	Yes	Reaching eye	Reddish brown with white speckling
9	<i>L. bijie</i>	29.0–30.4	Present	Rudimentary	Narrow	Shagreened and granular	Yes	Reaching to the middle of eye	White with distinct nebulous greyish speckling on chest and ventrolateral flanks
10	<i>L. botsfordi</i>	29.1–32.6	Absent	Rudimentary	Narrow	Shagreened	Yes	Reaching to middle of eye	Reddish brown with white speckling
11	<i>L. bourreti</i>	28.0–36.2	Present	Rudimentary	Narrow	Relatively smooth, some with small warts	Yes	/	Creamy white
12	<i>L. chishuiensis</i>	30.8–33.4	Present	Rudimentary	Narrow	Shagreened and granular	Yes	Reaching tympanum	White with distinct nebulous greyish speckling on chest and ventrolateral flanks
13	<i>L. crocea</i>	22.2–27.3	Absent	Rudimentary	Absent	Highly tuberculate	No	Reaching beyond tip of snout	Bright orange
14	<i>L. damingshanensis</i>	33.6–34.4	Present	Rudimentary	Narrow	Rough dorsal skin with sparse jacinth tubercles and some short longitudinal ridges	Yes	Reaching middle of eye	Creamy white ventral surface with small, creamy white glands on throat, chest and belly, becoming more concentrated near lateral margin
15	<i>L. dorsospina</i>	28.7–30.5	Present	Rudimentary	Narrow	Rough with dense conical granules, tubercles, glandular folds, and conical spines	Yes	Reaching to the posterior corner of eye	Greyish white with black spots and orange pigmentations
16	<i>L. eos</i>	33.1–34.7	Absent	Rudimentary	Wide	Shagreened	No	/	Creamy white
17	<i>L. feii</i>	21.5–22.8	Present	Rudimentary	Narrow	Shagreened with small tubercles and ridge	Yes	Reaching beyond eye, but not reaching snout	Creamy white with black blotches
18	<i>L. firrithi</i>	26.4–29.2	Absent	Rudimentary	Wide in males	Shagreened with fine tubercles	No	Reaching anterior margin of eye	Creamy white
19	<i>L. flaviglandulosa</i>	23.0–27.0	Present	Poorly developed	Narrow	Shagreened with yellowish brown tubercles	Yes	Reaching beyond eye, but not reaching snout	Whitish, black speckling on margins
20	<i>L. fuliginosa</i>	28.2–30.0	Present	Rudimentary	Narrow	Nearly smooth, few tubercles	Yes	Reaching anterior corner of eye	White with brown dusting

Continued Table S4

ID	Species	Males SVL (mm)	Black spots on flanks	Toes webbing	Lateral fringes on toes	Dorsal skin texture	Distinct dorsolateral markings	Tibiotarsal articulation	Ventral coloration
21	<i>L. graminicola</i>	23.1–24.6	Present	Rudimentary	Wide	Smooth, with many tubercles and lacking dermal ridges	Yes	Reaching to anterior edge of eye	White with very dark blackish brown spots
22	<i>L. isos</i>	23.7–27.9	Absent	Rudimentary	Wide in males	Mostly smooth, females more tuberculate	No	Reaching to nostril	Creamy white with white dusting on margins
23	<i>L. jinshaensis</i>	29.7–31.2	Present	Absent	Narrow	Shagreened and granular, some of the granules forming short longitudinal folds dorsally on the flank	Yes	Reaching to the middle of eye	Cream white
24	<i>L. kalonensis</i>	25.8–30.6	Present	Absent	Absent	Smooth	Yes	Reaching to anterior edge of eye	Pale, speckled brown
25	<i>L. khasiorum</i>	24.5–27.3	Present	Rudimentary	Wide	Isolated, scattered tubercles	Yes	/	Creamy white
26	<i>L. lateralis</i>	26.9–28.3	Present	Rudimentary	Absent	Roughly granular	Yes	/	Creamy white
27	<i>L. laui</i>	24.8–26.7	Present	Rudimentary	Wide	Round granular tubercles	No	Reaching anterior margin of eye	Creamy white with dark brown dusting on margins
28	<i>L. liui</i>	23.0–28.7	Present	Rudimentary	Wide	Round granular tubercles with glandular folds	Yes	Reaching anterior corner of eye	Creamy white with dark brown spots on chest and margins
29	<i>L. macrops</i>	28.0–29.3	Present	Rudimentary	Absent	Roughly granular with larger tubercles	No	Reaching eye	Greyish-violet with white speckling
30	<i>L. maculosa</i>	24.2–26.6	Present	Absent	Absent	Dorsum mostly smooth with numerous tiny tubercles	Yes	Reaching tip of snout	Brown, less white speckling
31	<i>L. mangshanensis</i>	22.2–27.8	Present	Rudimentary	Narrow	Nearly smooth, scattered tubercles	Yes	Reaching anterior margin of snout	White speckles on throat and belly
32	<i>L. maoershanensis</i>	25.2–30.4	Present	Rudimentary	Narrow	Shagreened with small tubercles and longitudinal ridges	Yes	Reaching well beyond anterior margin of eye	Creamy white chest and belly with irregular black spots
33	<i>L. melica</i>	19.5–22.7	Present	Rudimentary	Absent	Smooth	Yes	Reaching snout	Reddish brown with white speckling
34	<i>L. minima</i>	25.7–31.4	Present	Rudimentary	Absent	Smooth	Yes	/	Creamy white
35	<i>L. murphyi</i>	23.2–24.9	Present	Rudimentary	Wide	Shagreened with reddish tubercles and folds	Yes	Reaching beyond eye, but not reaching snout	Creamy white belly with small black spots on the margin
36	<i>L. nahangensis</i>	40.8	Present	Rudimentary	Absent	Smooth	Yes		Creamy white with light speckling on throat and chest
37	<i>L. namdongensis</i>	30.9	Present	Rudimentary	Absent	Finely tuberculate	No	/	Creamy white with brown dusting on margins
38	<i>L. neangi</i>	35.4–36.3 (in females)	Present	Weak (in females)	Absent (in females)	Dorsal skin with small, irregular bumps and ridges	Yes	Reaching just past anterior edge of eye (in female)	Light purplish gray with dark brown mottling on throat
39	<i>L. nokrekensis</i>	26.0–33.0	Present	Rudimentary	unknown	Tubercles and longitudinal folds	Yes	Reaching posterior corner of eye	Creamy white
40	<i>L. niveimontis</i>	22.5–23.6	Present	Rudimentary	Narrow	Relatively smooth with small tubercles	Yes	Reaching beyond eye, but not reaching snout	Marbling with black speckling
41	<i>L. nyx</i>	26.7–32.6	Present	Rudimentary	Absent	Rounded tubercles	No	/	Creamy white with white with brown margins
42	<i>L. oshanensis</i>	26.6–30.7	Present	Absent	Absent	Smooth with few glandular ridges	Yes	Reaching to the middle of eye	Whitish with no markings or only small, light grey spots
43	<i>L. pallida</i>	24.5–27.7	Absent	Absent	Absent	Tuberculate	No	Reaching to anterior edge of eye	Reddish brown with white speckling
44	<i>L. pelodytoides</i>	27.5–32.3	Present	Wide	Narrow	Small, smooth warts	Yes	/	Whitish

Continued Table S4

ID	Species	Males SVL (mm)	Black spots on flanks	Toes webbing	Lateral fringes on toes	Dorsal skin texture	Distinct dorsolateral markings	Tibiotarsal articulation	Ventral coloration
45	<i>L. petrops</i>	23.6–27.6	Absent	Absent	Narrow	Highly tuberculate	No	Reaching anterior edge of eye	Immaculate creamy white
46	<i>L. pluvialis</i>	21.3–22.3	Present	Rudimentary	Absent	Smooth, flattened tubercles on flanks	Yes	Reaching nostril	Dirty white with dark brown marbling
47	<i>L. puhoatensis</i>	24.2–28.1	Present	Rudimentary	Narrow	Longitudinal skin ridges	Yes	Reaching anterior edge of eye	Reddish brown with white dusting
48	<i>L. purpurus</i>	25.0–27.5	Present	Rudimentary	Wide	Shagreen with small tubercles	Yes	Reaching to posterior corner of the eye	Dull white with indistinct grey dusting
49	<i>L. purpuraventra</i>	27.3–29.8	Present	Rudimentary	Narrow	Shagreened and granular with dermal ridges	Yes	Reaching to the middle of eye	Grey purple with distinct nebulous greyish speckling on chest and ventrolateral flanks
50	<i>L. pyrrhops</i>	30.8–34.3	Present	Rudimentary	Absent	Slightly shagreened	Yes	/	Reddish brown with white speckling
51	<i>L. rowleyae</i>	23.4–25.4	Present	Absent	Absent	Mostly smooth	Yes	/	Pinkish milk-white to light brown chest and belly with numerous white speckles
52	<i>L. sungi</i>	48.3–52.7	Absent or small	Wide	Narrow	Granular	Yes	Reaching to the eye	White
53	<i>L. suiuyangensis</i>	28.7–29.7	Present	Rudimentary	Narrow	Shagreened with small granules	Yes	Reaching to the anterior eye	Yellowish creamy-white with marble texture chest and belly or with irregular light brown speckling
54	<i>L. shangsiensis</i>	24.9–29.4	Present	Rudimentary	Narrow	Mostly smooth with numerous tiny tubercles	Yes	/	Yellowish creamy-white with marble texture
55	<i>L. shiwandashanensis</i>	26.8–29.7	Present	Absent	Absent	Rough with numerous tubercles	Yes	Reaching to posterior of the eye	Creamy white
56	<i>L. tadungensis</i>	23.3–28.2	Present	Absent	Absent	Smooth	Yes	Reaching snout	Reddish brown with white speckling
57	<i>L. tamdil</i>	32.3	Present	Wide	Wide	Weakly tuberculate	Yes	/	White
58	<i>L. tengchongensis</i>	23.9–26.0	Present	Rudimentary	Narrow	Shagreened with small tubercles	Yes	Reaching to the middle of eye	White with dark brown blotches
59	<i>L. tuberosa</i>	24.4–29.5	Absent	Rudimentary	Absent	Highly tuberculate	No	/	White with small grey spots/streaks
60	<i>L. ventripunctata</i>	25.5–28.0	Present	Rudimentary	Absent	Longitudinal skin ridges	Yes	Reaching between the eye and the tympanum	Chest and belly with dark brown spots
61	<i>L. wulhuangmonis</i>	25.6–30.0	Present	Rudimentary	Narrow	Rough, scattered with dense conical tubercles	Yes	Reaching to the middle of eye	Greyish white mixed by tiny white and black dots
62	<i>L. wulingensis</i>	24.5–32.8	Small to moderate	Rudimentary	Narrow	Shagreened with sparse large warts, sometimes with longitudinal ridges	Yes	Reaching to the middle of eye	Creamy white, with distinct or indistinct brown speckling at margins
63	<i>L. yingjiangensis</i>	25.7–27.6	Present	Rudimentary	Wide	Shagreened with small tubercles	Yes	Reaching to the posterior corner of the eye	Creamy white with dark brown flecks on chest and margins
64	<i>L. yunkaicensis</i>	25.9–29.3	Present	Rudimentary	Wide	Shagreened with short skin ridges and raised warts	Yes	Reaching to the middle of eye	Belly pink with distinct or indistinct speckling
65	<i>L. yueae</i>	25.8–32.6	Present	Rudimentary	Narrow	Relatively smooth with tiny granules	Yes	Reaching to the middle eye	Cream white with small brown speckling on sides and upper abdomen
66	<i>L. zhangyapingi</i>	45.8–52.5	Absent	Rudimentary	Wide	Mostly smooth with distinct tubercles	Yes	Reaching to the middle of eye	Creamy-white with white with brown margins